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Recruitment into a local population of spruce grouse

by

(C)

Donald T. McKinnon

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Supervisor

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Date..... 4 October 1983..

Abstract

Three questions concerning recruitment into populations of spruce grouse were examined using data collected between 1965 and 1981 in southwestern Alberta. What factors influence the number of recruits into a local population? What factors influence the number of territorial recruits? Why do some yearling males take territories, whereas others do not? A positive correlation between the numbers of yearling females and males recruited suggests that both sexes are affected by the same factors or that these factors are correlated. The proportion of yearlings recruited of those available at the end of the winter appears to be regulated by the density of resident adults of the same sex. The results of a removal experiment support this hypothesis for both sexes. I was unable to show clear statistical relationships between number of territorial recruits and number of established territorial males or number of nonterritorial residents the previous year. The distribution of territorial male recruits on the study area following the removal of territorial adults was consistent with the spacing behaviour hypothesis. A comparison between territorial and nonterritorial yearling males suggested two hypotheses. 1)Yearlings that establish territories have higher blood androgen levels than nonterritorial yearlings. 2) Territorial yearlings disperse shorter distances than nonterritorial yearlings. These hypotheses need to be tested.

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INTRODUCTION

Recruitment may be defined as either an addition of individuals to a population or to a specific cohort within a population such as the territorial cohort. A first year resident is considered a recruit into the local population. A bird is a territorial recruit the first spring it exhibits territorial behaviour.

Changes in the number of grouse in spring appear to reflect changes in rates of recruitment in spruce grouse (Canachites canadensis) (Boag et al. 1979), blue grouse (Dendragapus obscurus) (Bendell 1972), and ruffed grouse (Bonasa umbellus) (Gullion 1970). Thus, factors influencing recruitment into a local population appear critical to understanding the dynamics of forest grouse populations.

In blue grouse, removal experiments have provided an insight into factors influencing recruitment. Experiments involving the removal of adults suggest that the number of yearlings recruited into a local population is regulated by the number of resident adults (Bendell and Elliot 1967, Bendell, King and Mossop 1972, Zwickel 1972). An alternative explanation, suggested by Zwickel (1980) after removal of yearlings, is that yearlings regulate their own numbers.

Less is known about recruitment into spruce grouse populations. A removal experiment conducted by Keppie (1979) suggests that the density of resident adults does not influence the proportion of yearlings that emigrate. Boag et al. (1979) postulated that the number of recruits into a

local population may be a function of production the previous year. They provided some evidence that the proportion of yearlings recruited of those available was inversely correlated with the number of resident adults.

Yearling female spruce grouse are territorial (Herzog and Boag 1978); thus recruitment into a local population and territorial recruitment occur the same year (Herzog and Boag 1978). However, among males, territorial recruitment usually occurs when the grouse are first year adults (Herzog and Boag 1978), the year after recruitment into a local population. Thus, recruitment can be studied separately from recruitment into a local population only in males.

Nonterritorial male ruffed grouse and blue grouse may take territories if vacancies are created (Boag 1976, Lewis and Zwickel 1980). Territorial recruitment may, therefore, be regulated by the spacing behaviour of established territorial males in these species.

Spruce grouse are suitable for population studies because they are easily approached, captured and individually marked and the number of recruits and established residents can be counted with confidence. The population used in this investigation had been studied for several years by previous workers (McCourt 1969, McLachlin 1970, Keppie 1975, Herzog 1977, and Nugent 1979), providing data on the dynamics of the population and the background of its individuals.

This study was designed to address three questions about recruitment into populations of spruce grouse. What factors influence the number of recruits into a local population? What factors influence the number of territorial recruits? Why do some yearling males take territories, whereas others do not?

The results are presented in two chapters:

1. Factors influencing recruitment into a local population and territorial recruitment of Franklin's spruce grouse, and

2. Dispersal histories, physical attributes, and age-specific survival rates of nonterritorial and territorial yearling male Franklin's spruce grouse.

GENERAL METHODS

My study encompassed three field seasons, beginning in mid-May 1979, mid-April 1980 and 1981, and ending in late August or early September of each year.

Three census methods outlined in Boag and McKinnon (1982) were used: playbacks of a female cantus (Nugent and Boag 1982) helped locate males and occasionally females in 1979. This technique was not used in 1980 or 1981 because it attracted birds and, therefore, could bias estimates of the location of territorial space. Dawn and dusk censuses were conducted in 1980 and 1981 during peak territorial advertisement in spring. Territorial males were more easily located at these times because they frequently perform auditory flight displays (wing claps and flutter flights) (Nugent 1979). This technique was very successful for approximately 2 weeks in 1980 (10 May - 24 May), and for approximately 9 weeks in 1981 (20 April - 22 June). The third method consisted of walking compass-directed transects across the study area. Pointing dogs were used in August 1979 and in 1980 and 1981.

Unmarked birds were caught with a noosing pole (Zwickel and Bendell 1967) and marked with a unique combination of coloured leg bands. Sex, band combination, date, time and observer were written on a piece of surveyor's tape that was tied to a tree as close as possible to the location where the grouse was first sighted. Sighting locations were estimated from a gridded air photo (1:5000) of the study

area. Other sightings were estimated by determining the compass direction and distance from marked locations.

Yearling (6 - 15 months) and adult (>15 months) spruce grouse were classified by the method of McCourt (1969) and McLachlin (1970), which involved the total lengths and shaft diameters of the first primaries, central rectrices and upper central tail coverts. Following their moult, shaft diameters of ninth primaries were used for age determination (McKinnon 1983).

Males that were seen displaying were considered territorial. In 1980 and 1981, a behavioural test (MacDonald 1968) was conducted to determine the territorial status of males not seen displaying. A mounted female spruce grouse and cassette tape recorder were placed on the ground 10 meters from the male. The tape recorder was switched on and the observer retreated about 10 meters. The first 3 minutes of the tape were blank, followed for the next 5 minutes by a female cantus. The female cantus attracted territorial males to the vicinity of the mounted female. Display to the female was considered evidence of territoriality.

Data collected by previous graduate students (McCourt 1969, McLachlin 1970, Keppie 1975, Herzog 1977, Nugent 1979, and Smyth 1983) were used in this study.

STUDY AREA

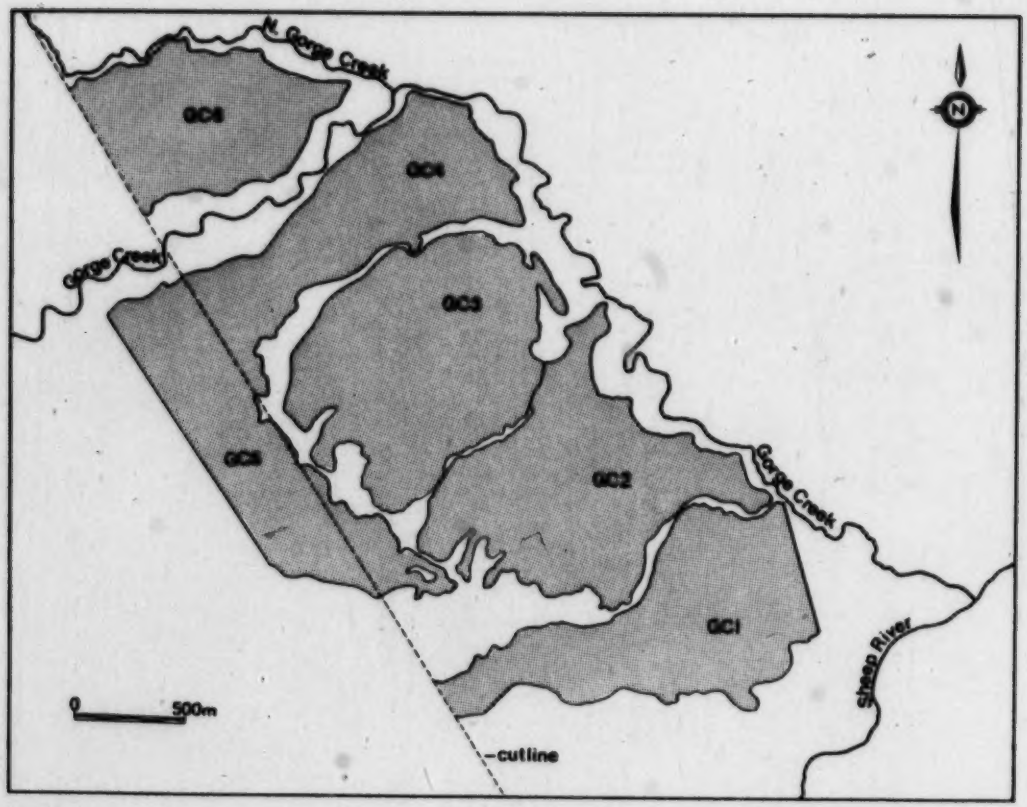
The study area, 27 km west of Turner Valley, Alberta, is in the eastern foothills of the Rocky Mountains. In the 1960's, McCourt (1969) and McLachlin (1970) described the vegetation on this area. They recognized four types: 1) lodgepole pine forest (Pinus contorta) covering 72% of the area, 2) mixed forest composed of aspen (Populus tremuloides) and balsam popular (P. balsamifera), 3) spruce forest composed of white spruce (Picea glauca) and lodgepole pine, and 4) meadow-marsh. This description reflects the composition of the vegetation on the area during this study. However, tree heights and stem diameters have increased and stem densities have decreased in the lodgepole pine forest since the 1960's. Succession also has advanced in the other vegetation types.

The study area was divided into six sections, referred to as GC1 through GC6. Some boundaries of the sections have been changed as different workers sought answers to different questions. McCourt (1969) and McLachlin (1970), worked a "main study area" of approximately 300 ha in 1965, which they expanded to approximately 600 ha for 1966 - 1968 (Fig. 1). In 1969, the study area was not censused. Keppie (1975) altered the western and northern boundaries of the "main study area", censusing an area of 550 ha (Fig. 2). In 1970, GC6 was not thoroughly censused. Herzog (1977) censused the same sections as Keppie (1975) except that the boundaries of GC5 were different. He concentrated his

Figure 1. Location of the "main study area" used by McCourt (1969) and McLachlin (1970) during the period, 1966 - 1968.

Snake River
Gorge Creek
GC1
GC2
GC3
GC4
GC5
GC6
N Gorge Creek
cutline
Gorge Creek
N
500m

Figure 2. The study area used by Keppie (1975) during the period, 1970 - 1973.


N. Gorge Creek
GC6
GC4
Gorge Creek
GC3
GC5
GC2
Gorge Creek
GC1
Sheep River
0 500m
cutline

efforts on two sections each year (1974: GC3 and GC5; 1975: GC1 and GC3). Nugent (1979) concentrated his censusing on GC1 and GC6 in 1976 and 1977. In 1978, GC1, GC4 and GC6 were censused, plus the eastern parts of GC2 and GC3 (Fig. 3). The latter boundaries were retained in the 1979 - 1981 field seasons. This area was used for my removal experiments. A core study area (core area), censused in all years from 1965 to 1981, at least in part (except 1969), included GC1 and the eastern parts of GC2, GC3, and GC4, an area of 247 ha (Fig. 4). The population on this block of habitat was used in the analysis of factors influencing recruitment.

Figure 3. The study area censused during the period, 1978 - 1981.

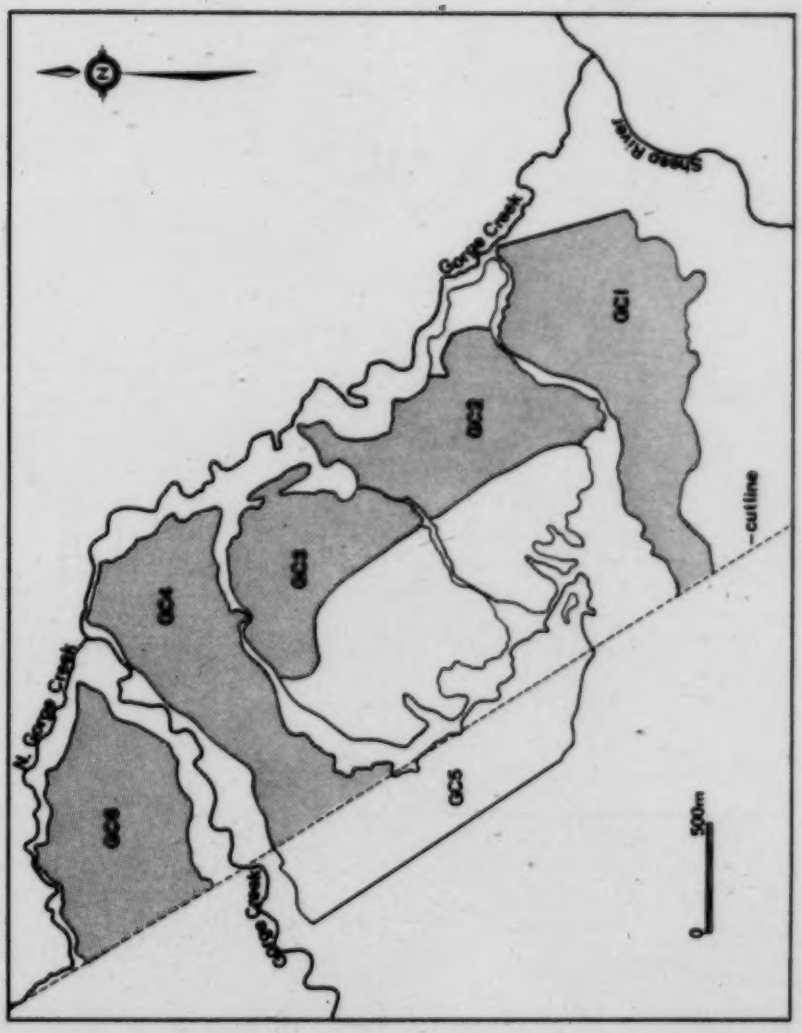
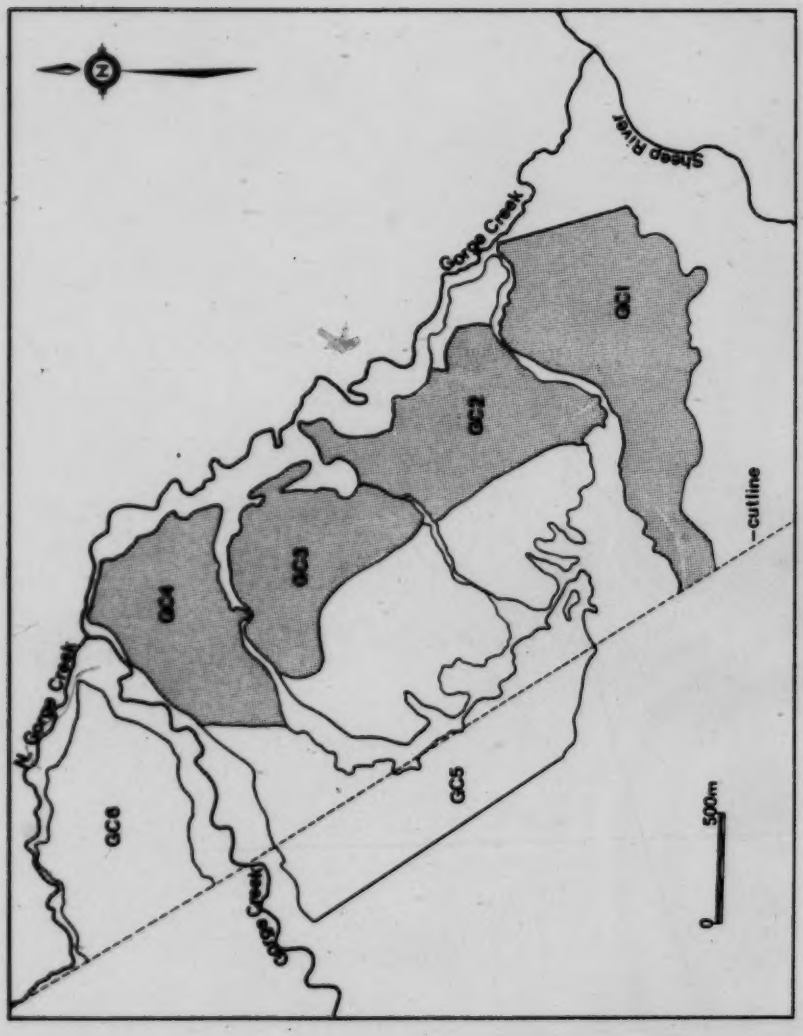

N
Snipe River
George Creek
OC1
OC2
OC3
OC4
OC5
OC6
-cutline
500m
0
Mt George Creek
George Creek

Figure 4. A core study area that was censused in most years from 1965 - 1981.


N
Sheep River
Gorge Creek
GC1
GC2
GC3
GC4
GC5
GC6
-cutline
N. Gorge Creek
Gorge Creek
0
500m

CHAPTER 1. Factors influencing recruitment into a local population and territorial recruitment of Franklin's spruce grouse

Introduction

Spring densities of tetraonid populations may cycle, fluctuate irregularly, or remain relatively stable (Watson and Moss 1979). Population ecologists try to identify those factors that account for the dynamics of populations.

A population of Franklin's spruce grouse (Canachites canadensis franklinii) occupying 247 ha in the southwestern foothills of Alberta (the Gorge Creek (GC) study area) has been studied for all but one breeding season between 1965 and 1981 (McCourt 1969, McLachlin 1970, Keppie 1975, Herzog 1977, Nugent 1979, Smyth 1983, this study). Spring density of this population remained relatively stable (varying by less than 3 grouse per 100 ha) from 1971 to 1974, following a period of population growth between 1965 and 1971 (Boag et al. 1979). This stability implies that the population was regulated (Zwickel and Bendell 1972). Population regulation occurs when a negative feedback mechanism operates in a population to maintain a particular density.

Using correlative evidence, Boag et al. (1979) suggested two mechanisms by which regulation was achieved in this population. Firstly, the number of juveniles surviving to September declined as the density of females resident during the breeding season increased. This relationship,

however, was not sustained when data collected after 1975 were included (Smyth 1983). Secondly, the number of yearlings recruited each year was negatively correlated with the density of adults at the onset of the breeding season, as a consequence of the spacing behaviour of the residents. This held the number of resident birds almost constant. Spacing behaviour has been described for both sexes (Herzog and Boag 1978). Since intraspecific aggression has only been reported between individuals of the same sex (Alway 1977), this negative feedback system was assumed to operate independently for each sex.

Recruitment into this population can be perceived as a two-phase process: initial establishment of yearlings into the local population and subsequent establishment of a territory once recruited onto the area (territorial recruitment). Males typically establish territories as first year adults whereas females are usually territorial as yearlings (Herzog and Boag 1978). Thus factors influencing recruitment at both stages can be examined separately most easily for males.

The first objective was to determine the numbers and age composition of spruce grouse of each sex at the start of each breeding season on a block of habitat that was censused in most years between 1965 and 1981. By considering a common block of habitat, among-year variation in density can not be attributed to differences in the habitat of areas censused, a potentially important factor not completely controlled for

by Boag et al. (1979).

Secondly, I searched for factors influencing the number of yearling spruce grouse being recruited into the local population. The following evidence was considered:

a) the relationship between numbers of yearlings and adults at the onset of the breeding season; (Boag et al. (1979) reported an inverse relationship between numbers of yearling and adult spruce grouse. I examined this relationship with the addition of data from later years from the same area.),

b) the relationship between the proportion of yearlings recruited of those available at the end of the winter (31 March) and number of adults of the same sex on the core area (Boag et al. (1979) reported an inverse relationship between recruitment rates of yearlings and adult density, based on 3 years data. I examined this relationship with data from additional years),

c) the results of a removal experiment to test whether spacing behaviour of adults regulated population recruitment of yearlings of the same sex into the local population, and

d) the relationship between number of yearlings recruited in one year and number of young produced the previous year. In Michigan, recruitment of yearling spruce grouse was considered independent of number of chicks produced the previous year (Robinson 1980). This conclusion was based on variation in number of yearling and age unknown (assumed to be yearling) grouse among years despite

production apparently being relatively stable. However, a relationship may have been obscured by incorrectly assuming that birds of unknown age were yearling recruits.

Thirdly, I searched for factors influencing the number of male spruce grouse that established territories in the local population (territorial recruitment). The following evidence was considered:

a) the relationship between the numbers of newly recruited and established territorial males at the onset of each breeding season,

b) the results of a removal experiment conducted to test whether spacing behaviour of territorial males regulated territorial recruitment, and

c) the relationship between number of males recruited into the territorial cohort and number of nonterritorial resident males present the previous year.

Methods

Numbers of resident male and female spruce grouse were determined for a 247 ha core area that had been censused for 12 of 17 years, from 1965 - 1981.

The centre of the area occupied by each bird was estimated by a median location. This was the intersection of the median values of all the x and y coordinates of sightings for each individual. These were plotted on a gridded aerial photograph of the study area. If a bird's median location was in the core area it was considered a

resident. Only locations of sightings made between 15 May and 15 August were used for estimating the median location of adult females and yearlings of both sexes in order to exclude locations of adult females during migration (Herzog and Keppie 1980) and yearlings before they established home ranges. Most adult males were on the summer range in early spring (Herzog and Boag 1978), so locations from 15 April to 15 August were used to calculate their median locations. Males seen only between 15 April and 14 May were not considered residents of the core area but only migrants.

A bird was assumed to have been a resident in a given year despite not being seen, if it had been resident the previous and following years. This assumption was made 10 times (3.9%) for females and once (0.4%) for males during the 12 years that the core area was censused.

Birds first observed following the breeding season (16 August - 4 September) were assumed to have been residents if located in approximately the same area the next breeding season. This assumption was made five times (2.0%) for females and twice (0.7%) for males. Some birds were not considered residents because they were recorded on the core area, in other years, only before and/or after the breeding season (15 May - 15 August). This assumption was made once for females (0.4%) and twice for males (0.7%).

Based on the relationship between numbers of each sex-age group in GC1 and the rest of the study area for the 12 years in which all sections of the core area were

censused, the numbers on the core area were estimated for another 4 years (1965 and 1975 to 1977) when numbers were known only for GC1.

Chick production was based on brood counts for females with chicks 4 weeks of age or older on and off the core area. It was recorded in two ways: 1) mean number of chicks produced per female, and 2) total number of chicks produced on the core area. Number of chicks produced per female was defined as the total number of chicks 4 weeks of age or older divided by the total number of females seen after the nesting period. Number of chicks produced on the core area was calculated by multiplying the number of chicks per female by the number of resident females on the core area.

The number of yearlings present on the core area at the end of winter (31 March) was estimated using the number of juveniles produced; a good estimate of the number of birds on the area at the start of winter (Keppie 1979). This number was multiplied by the mean overwinter survival rate (0.87) (Keppie 1979) to estimate the number of yearlings present at the end of winter. Assuming a 1:1 sex ratio (Keppie 1979), the total number of surviving yearlings was halved to estimate the number of yearlings of each sex.

The relationship between the number of yearlings recruited as a percent of those available and number of adults was calculated with and without data for 1966 and 1975. This was done because additional estimates were required to arrive at the numbers present for these 2 years.

The number of juveniles produced in 1965, which was used to estimate the number of yearlings available in 1966, was based on an estimate of the number of females on the core area. Likewise, the number of adults in 1975 was estimated from the number on GC1.

Based on locations where grouse were sighted in 1979, nine aggregates of grouse were identified on the study area. Three of these were left unmanipulated as controls, and two were used for each of the following purposes: removal of males, removal of females, and removal of males and females.

Nine adult males and six adult females were removed from different subsections of the study area between 12 August and 1 September, 1979. A seventh adult female was killed accidentally on 10 July, 1979. These birds were removed in late summer to preclude any influence they may have had on recruitment of yearlings the following spring.

All adult males were considered territorial and most yearling males nonterritorial (McLachlin 1970: p.57). Yearlings that wing-clapped or performed flutter-flights were considered territorial. If an adult male was not observed displaying this was not considered sufficient evidence to classify it as nonterritorial. Males of unknown age were assumed to be yearlings. Thus, those males of unknown age that were not seen displaying were considered nonterritorial. Residents holding a territory in the previous year are referred to as established territorial males.

Relationships between parameters were examined with simple linear regressions or Pearson's correlations. Computer simulations were conducted to determine if the observed distribution of recruits on the study area deviated significantly from the distribution expected based on the spacing behaviour hypothesis. Differences were considered significant when $P \leq 0.10$. Since sample sizes were small, this significance level was used to reduce the probability of committing Type II errors (Tacha et al. 1982).

Results

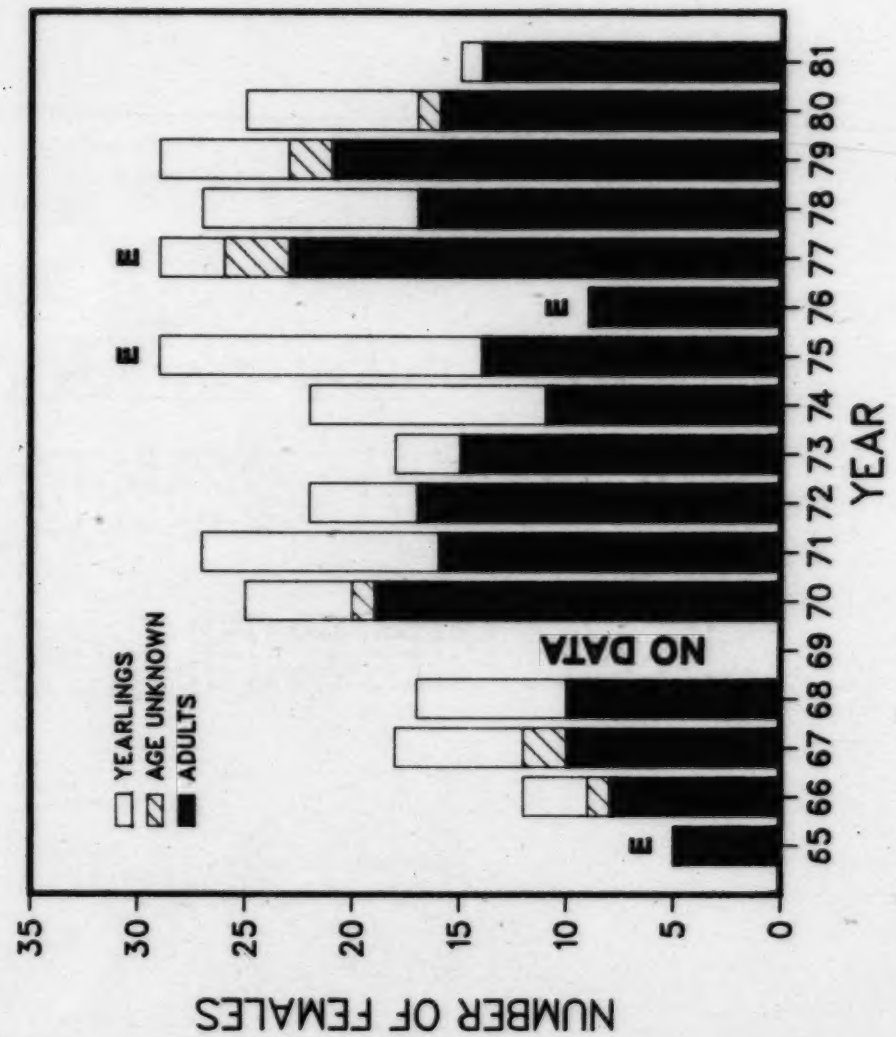
Recruitment of yearling spruce grouse into a local population

Females

Numbers and age structure of females counted in or estimated for the core area for 16 of 17 years from 1965 - 1981 are shown in Figure 1. The number of females estimated in 1976 is not considered representative as the census of GC1 was thought to have been incomplete and the data for this year are excluded from further analyses.

Numbers of females ranged from 5 (1965) to 29 (1975, 1977, and 1979). By excluding the years following the removal of birds in 1979, plus 1965 and 1975 to 1977 when numbers were estimated from counts of GC1, the minimum becomes 12 (1966) and the maximum remains 29. This represents a 2.4-fold change in number of females.

Figure 1. Number of female spruce grouse on the core area at the onset of the breeding season, 1965 - 1981. E indicates that numbers were estimated from counts of GC1.


NUMBER OF FEMALES
0
5
10
15
20
25
30
35
YEAR
65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81
NO DATA
E
E
E
E
YEARLINGS
AGE UNKNOWN
ADULTS

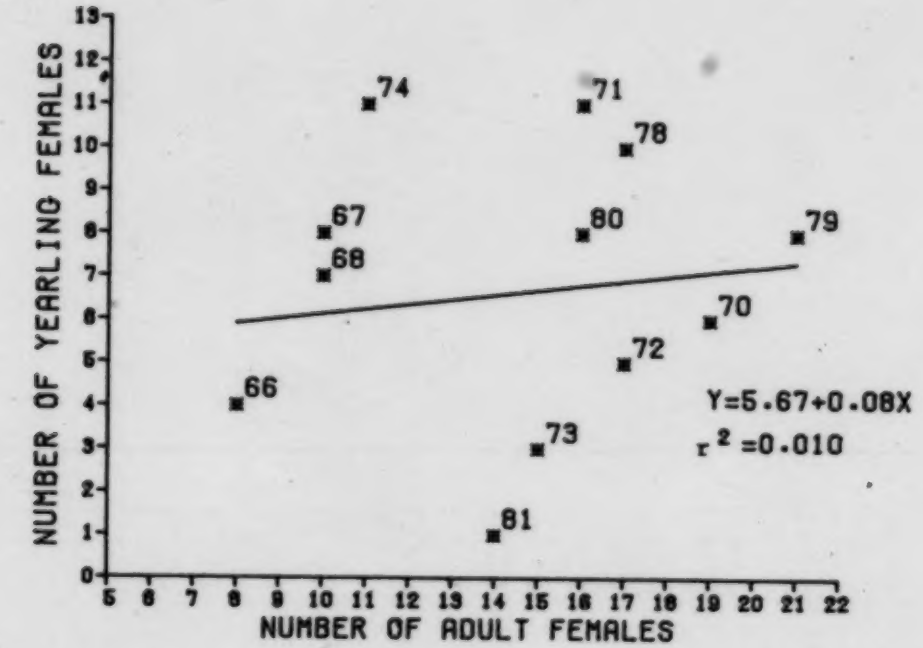
Numbers of females have been more stable since 1970. If data for 1980 and 1981, following the 1979 removal, and 1975 to 1977 when numbers were estimated from counts of GC1 are excluded numbers of females ranged from 18 (1973) to 29 (1979), which is a 1.6-fold change. The age of all females on the core area was determined for 8 years. Mean number of yearlings was 7 and adults 15, a ratio of 1:2.1. Number of adult females has ranged from 10 (1968) to at least 21 (1979), and yearling females from 1 (1981) to 11 (1971 and 1974).

The relationship between the numbers of adult females and yearling females was examined for all years and years when numbers were most stable (1970 - 1979) (Fig. 2). The slope, 0.08, is not significantly different from 0 (ANOVA, $F=0.103$; $P=0.755$). When only the more stable years are considered, this relationship becomes inverse (slope=-0.27), but not significantly so (ANOVA, $F=0.0381$, $P=0.564$). These data do not support the hypothesis of Boag et al. (1979) that number of resident adult females regulates the number of yearling females.

However, when the relationship between number of yearling females recruited as a percent of those available prior to spring dispersal and number of adult females was examined (Fig. 3), a slope of -8.83, significantly different from 0 (ANOVA, $F=4.774$; $P=0.065$), was found. Excluding the data for 1966 and 1975, since additional estimates were necessary, the slope of the regression line was -10.71 and

Figure 2. Relationship between numbers of adult and yearling female spruce grouse at the onset of the breeding season from 1966 - 1981 (A) and 1970 - 1979 (B); birds of unknown age were assumed to be yearlings.

A


NUMBER OF YEARLING FEMALES
NUMBER OF ADULT FEMALES
74
71
78
67
80
79
68
70
72
66
73
81
Y=5.67+0.08X
r 2 =0.010

B

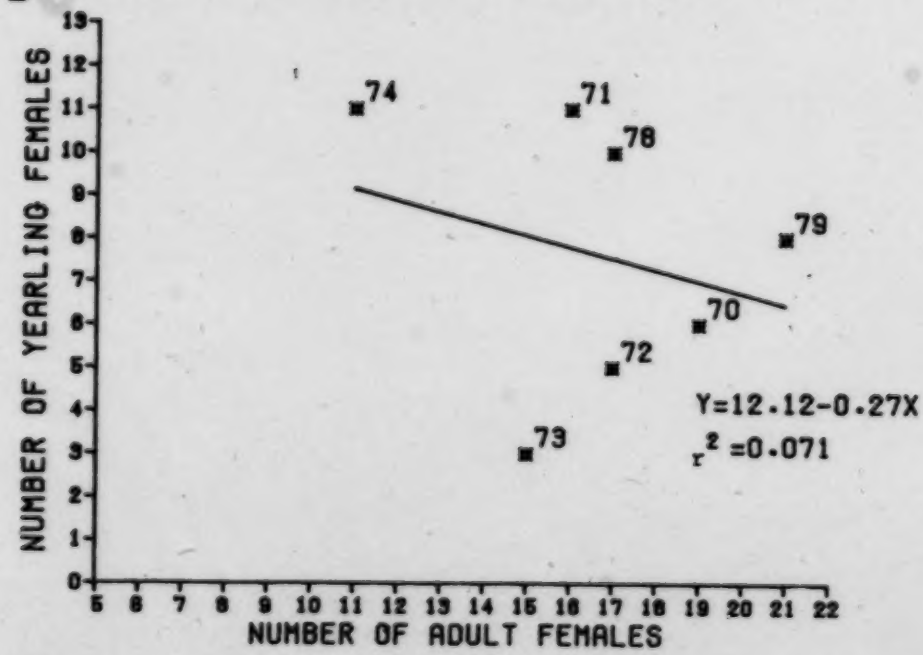
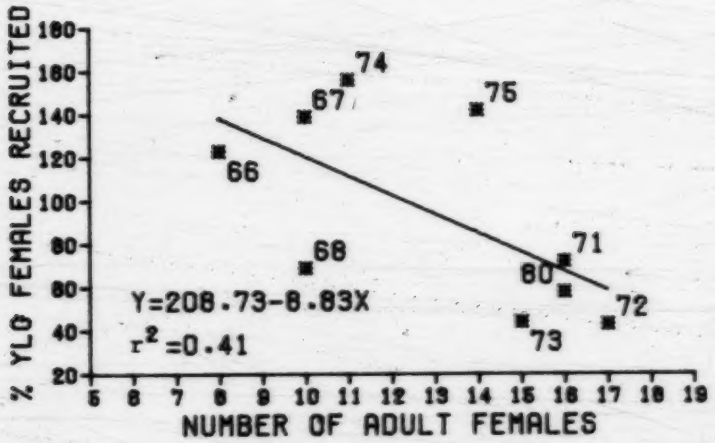
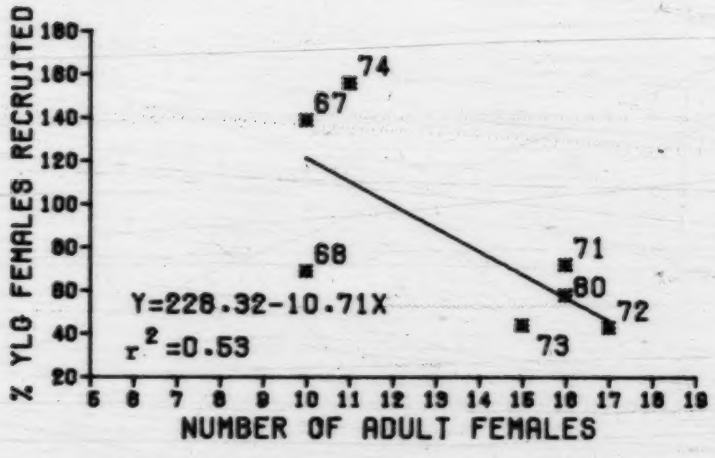

NUMBER OF YEARLING FEMALES
NUMBER OF ADULT FEMALES
74
71
78
79
70
72
73
Y=12.12-0.27X
r 2 =0.071

Figure 3. Relationship between percent of yearling female spruce grouse recruited of those available prior to spring dispersal, and number of adult females on the core area for 1966 - 1980 (A), and excluding data for 1966 and 1975 (B).

A


% YLO FEMALES RECRUITED
NUMBER OF ADULT FEMALES
Y=208.73-8.83X
r²=0.41
66
67
68
74
75
71
80
72
73

B


% YLO FEMALES RECRUITED
NUMBER OF ADULT FEMALES
Y=228.32-10.71X
r²=0.53
67
68
74
71
80
72
73

was significantly different from 0 (ANOVA, $F=5.598$, $P=0.064$). These results suggest that the proportion of potential yearling females recruited decreased as the number of resident adult females increased. This suggests that adult females regulated recruitment of yearling females.

Males

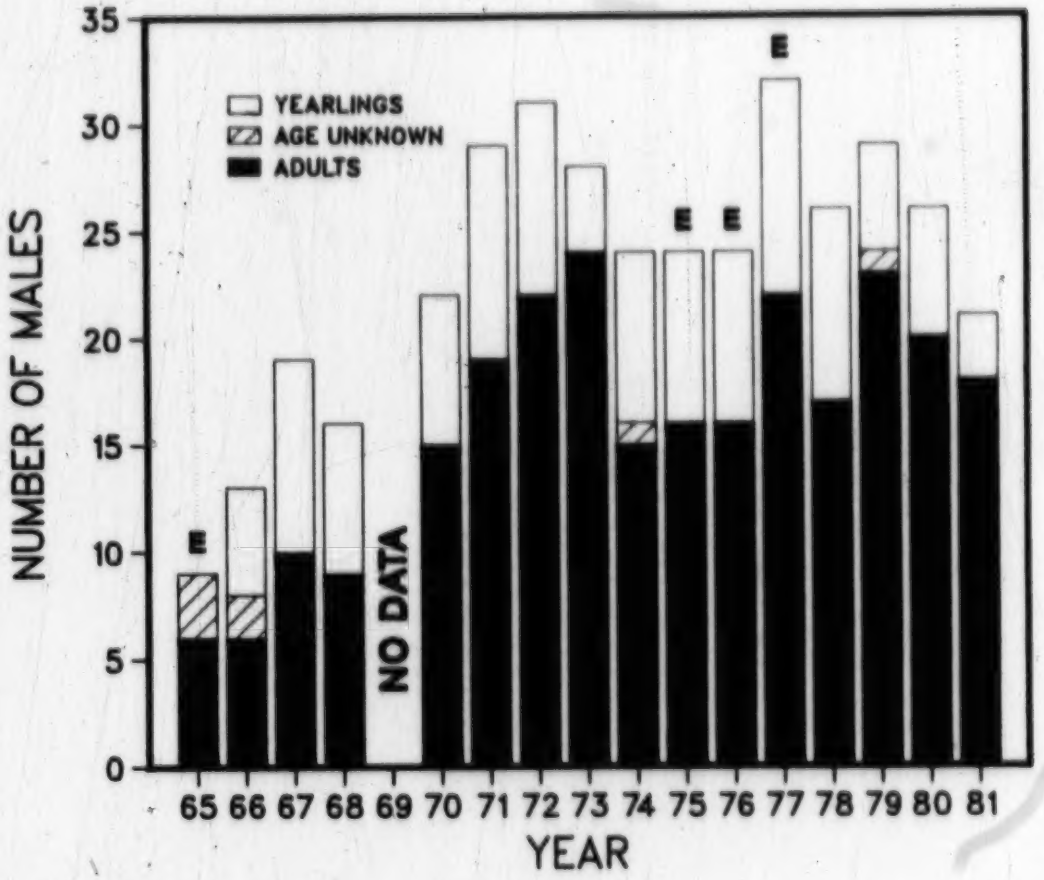
Numbers and age structure of males counted in or estimated for the core area for 16 of 17 years from 1965 - 1981 are shown in Figure 4. Numbers of males ranged from 9 (1965) to 32 (1977). Excluding years following the removal of birds in 1979 (1980 and 1981) plus 1965 and 1975 to 1977 when numbers were estimated from counts of GC1, the minimum and maximum become 13 (1966) and 31 (1972), respectively. As with females, this represents a 2.4-fold change in numbers.

Number of males has been more stable since 1970, ranging from 21 (1981) to 32 (1977). Excluding the years following the removal of birds in 1979 plus 1965 and 1975 to 1977 when numbers were estimated from counts of GC1, the numbers still range from 22 (1970) to 31 (1972), which is a 1.4-fold change, similar to that of females.

In years when the age of all males on the core area was determined the mean number of yearlings was 7 and adults, 17, a ratio of 1:2.4, similar to that of females. The numbers of adult males has ranged from 9 (1968) to 24 (1973) and yearling males from 3 (1981) to 10 (1971).

The relationship between the number of adult and yearling males on the core area at the onset of the breeding

Figure 4. Number of male spruce grouse on the core area at the onset of the breeding season, 1965 - 1981. E indicates that numbers were estimated from counts of GC1.


YEARLINGS
AGE UNKNOWN
ADULTS
NUMBER OF MALES
35
30
25
20
15
10
5
0
E
E
E
E
NO DATA
65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81
YEAR

season was examined with a simple linear regression for all years and those years when numbers were more stable (1970 - 1979) (Fig. 5). In the former case, the slope, -0.12 was not significantly different from 0 (ANOVA, F=1.018; P=0.337). A slope of -0.31, based on the years 1970 - 1979, was also not significant (ANOVA, F=2.123; P=0.205). As with females, these data do not support Boag et al.'s (1979) hypothesis that the number of resident adult males regulated the number of yearling males recruited.

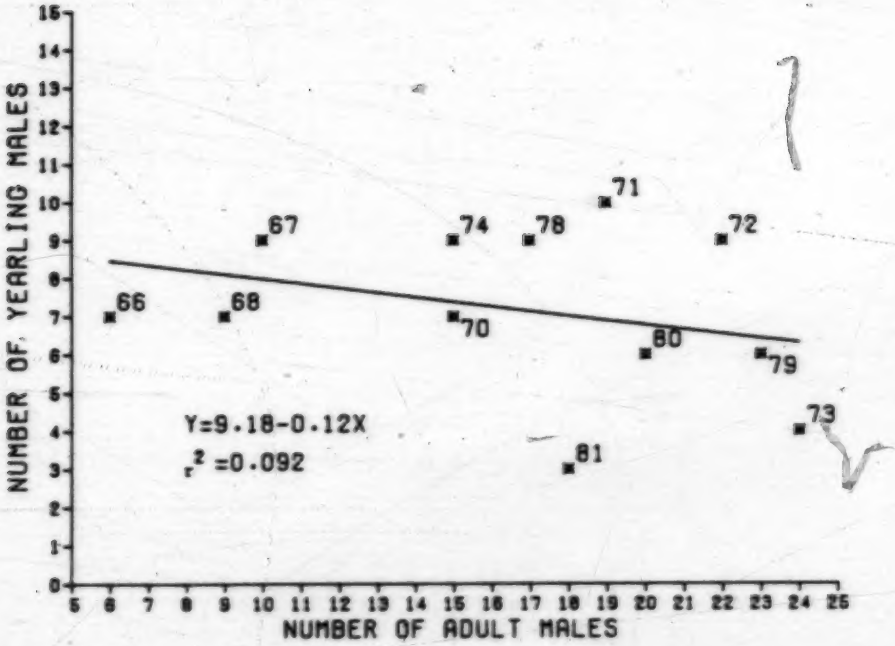
However, when the relationship between the number of yearling males recruited as a percent of those available before spring dispersal and number of adult males present on the core area was examined with simple linear regressions (Fig. 6), a slope of -6.46 significantly different from 0 (ANOVA, F=6.383; P=0.039), was found. However, excluding the data for 1966 and 1975, when additional estimates were necessary, the slope of the regression line becomes -3.46 which was not different from 0 (ANOVA, F=1.490; P=0.277). When all available data were included, the proportion of potential yearling males recruited decreased as the number of adult males increased. This suggests that adult males regulated recruitment of yearling males.

Removal Experiment

A removal experiment was conducted to test the hypothesis that the number of yearlings recruited was regulated by the number of resident adults of the same sex (spacing behaviour hypothesis). Accordingly, the number of

Figure 5. Relationship between numbers of adult and yearling males at the onset of the breeding season for 1966 - 1981 (A) and 1970 - 1979 (B); birds of unknown age were assumed to be yearlings.

A


NUMBER OF YEARLING MALES
NUMBER OF ADULT MALES
Y=9.18-0.12X
r² =0.092
66
67
68
70
71
74
78
72
60
79
81
73

B

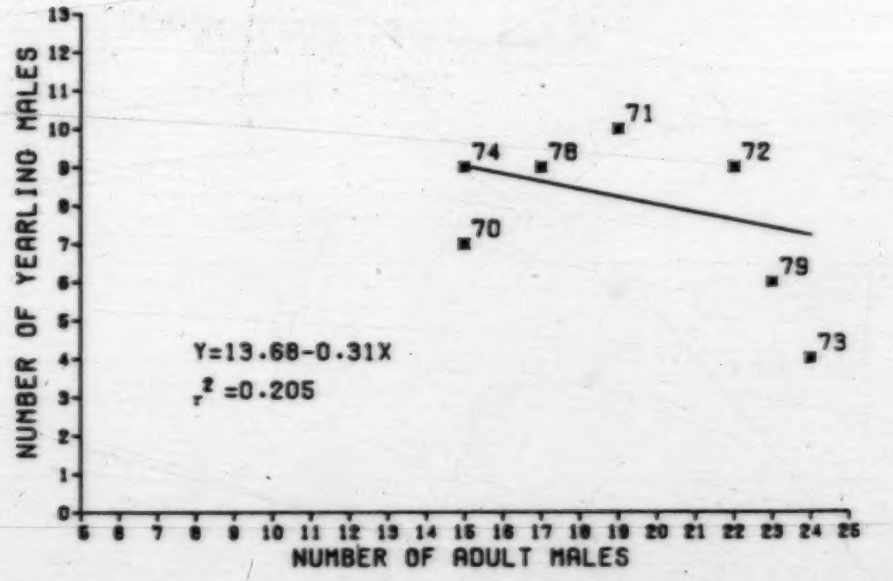
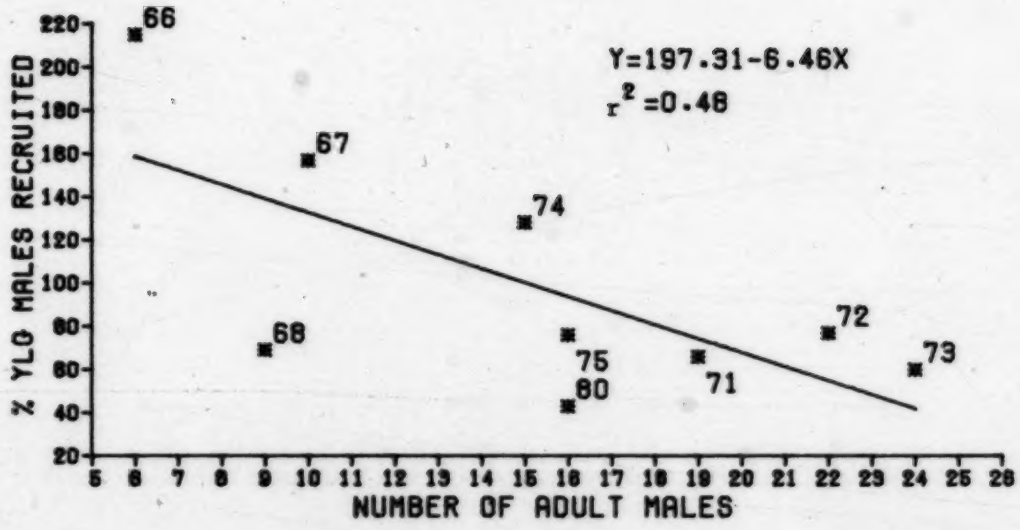
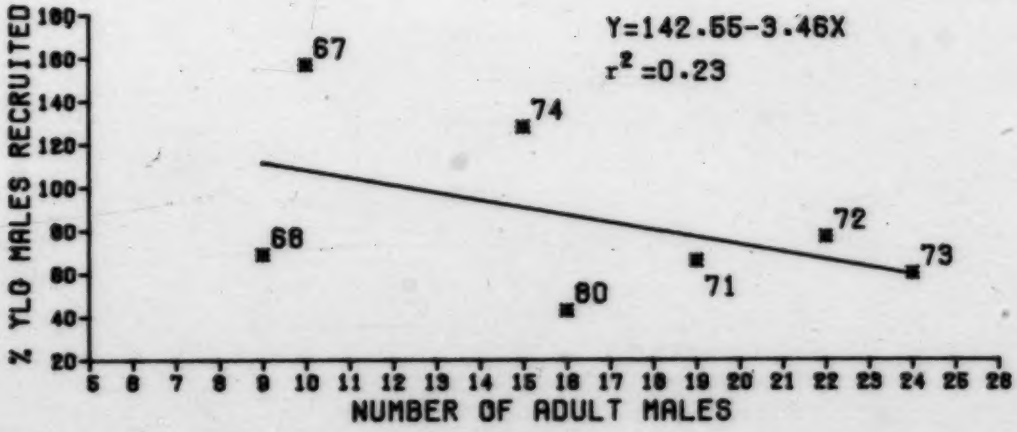

NUMBER OF YEARLING MALES
NUMBER OF ADULT MALES
Y=13.68-0.31X
r² =0.205
70
71
74
78
72
79
73

Figure 6. Relationship between percent of yearling male spruce grouse recruited of those available prior to spring dispersal, and number of adult males on the core area for 1966 - 1981 (A) and excluding data for 1966 and 1975 (B).

A


Y=197.31-6.46X
r² =0.46
% YLO MALES RECRUITED
NUMBER OF ADULT MALES
66
67
74
68
72
73
75
80
71

B


Y=142.55-3.46X
r² =0.23
% YLO MALES RECRUITED
NUMBER OF ADULT MALES
67
74
72
68
73
71
80

birds on each of the subsections in 1979 are assumed to have been at carrying capacity for that habitat in that year. If annual changes in carrying capacity in these areas fluctuate in parallel, one would predict that, as the number of territorial individuals removed from an area increased, resistance to recruitment through spacing behaviour would be reduced. Consequently, if spacing behaviour of territorial adults were regulating recruitment of yearlings, more recruits would be expected on those areas where more resident adults had been lost.

Numbers of female recruits were expected to be distributed among the subsections in proportion to the number of vacancies in each area (Table 1). The number of vacancies was defined as the difference between the number of females resident in 1979 and the number of those birds that returned 1980. The probability of recruitment into a subsection was considered to be the proportion of the total number of vacancies on the study area, which were in that subsection.

A computer simulation was conducted to determine if the observed distribution of recruits deviated significantly from the distribution expected from the spacing behaviour hypothesis. Based on the probability of recruitment in each subsection, distributions of recruits were randomly selected. 1,362 of the 10,000 simulated distributions had lower probabilities of occurrence than the observed distribution. Thus, the observed distribution did not depart

Table 1. Number of female spruce grouse removed and lost from and recruited onto various subsections of the study area, 1979 - 1980.

Subsection	Present in 1979			Lost					Recruited	Present in 1980		
				Removed		Disappeared		Total				
	Ylg	Ad	Total	Ylg	Ad	Ylg	Ad			Ylg	Ad	Total
Control												
1	1	3	4	0	0	0	2	2	1[1]	0	3	3
4	0	6	6	0	0	0	1	1	1	1	5	6
9	2	2	4	0	0	0	2	2	0	0	2	2
Male and Female Removal												
2	1	4	5	0	2	0	2[1]	4	1	1	1	2
3	1	3	4	0	1	0	1	2	2	1	3	4
Male Removal												
5	4	3	7	0	0	2	3[1]	5	2	2	2	4
8	0	5	5	0	0	0	2	2	3[2]	2	4	6
Female Removal												
6	2	2	4	0	1	0	0	1	2[2]	1	4	5
7	0	4	4	0	3	0	1	4	1	1	0	1
	11	32	43	0	7	2	14	23	13	9	24	33

[1] one adult moved to another section.

[2] one adult recruit.

significantly from the expected distribution (P=0.1362). This result weakly supports the spacing behaviour hypothesis.

Since yearling males are usually nonterritorial they are not considered replacements of the territorial adults. Consequently, the analysis used for females is not appropriate. A less rigorous approach comparing changes in number of adults in different areas between years and subsequent yearling recruitment was adopted. The change in number of adults from 1979 to 1980 was +2 (1979 - 13; 1980 - 15) and -7 (1979 - 20; 1980 - 13) in the control and removal areas, respectively. Removal areas were those subsections from which adult males had been removed. Consistent with the spacing behaviour hypothesis, 8 of 9 yearling males recruited onto the removal areas (Table 2).

Relationship between numbers of yearling males and females recruited

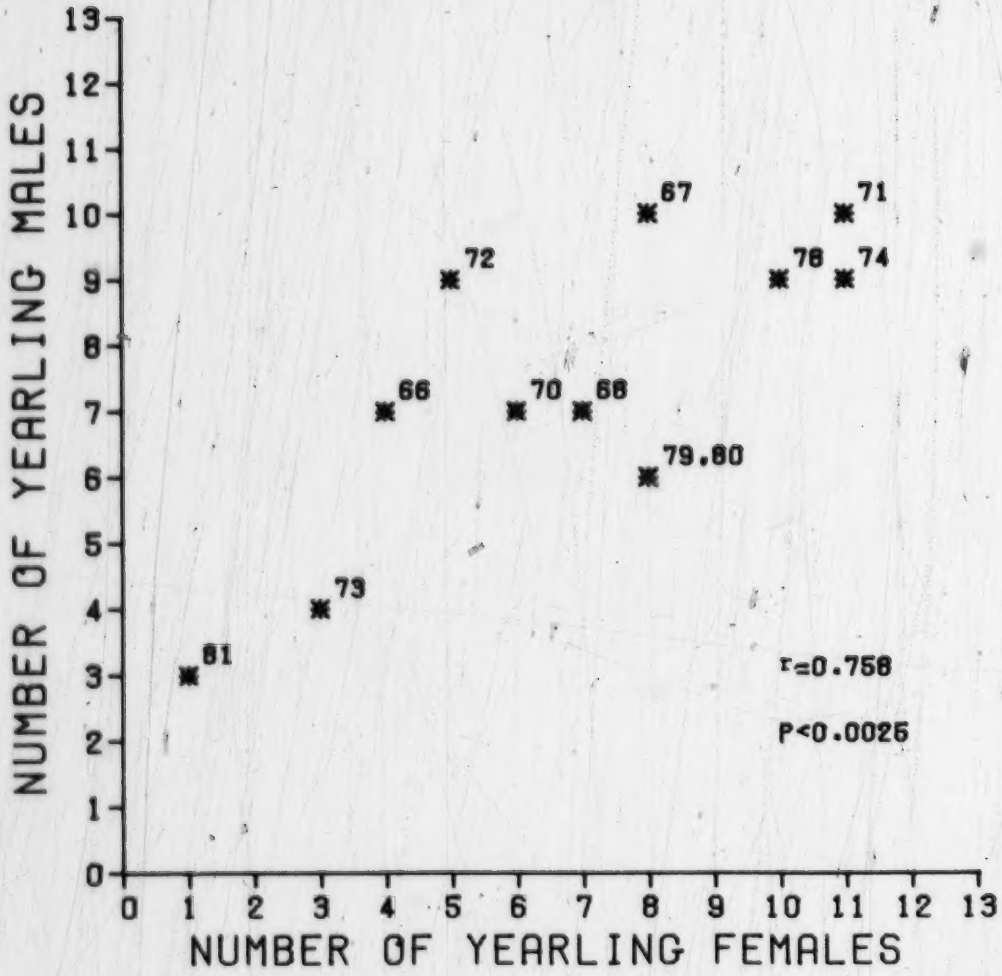
The number of yearling males recruited each year was compared to that of females recruited (Fig. 7), and found to be positively correlated (r=0.758; P<0.0025). This result suggests that the factors influencing the numbers of yearling males and females recruited into a local population are either correlated or the same. A potential common factor is the number of young produced the previous breeding

Table 2. Number of male spruce grouse removed and lost from and recruited onto various subsections of the study area, 1979 - 1980.

Subsection	Present in 1979			Lost					Recruited	Present in 1980		
				Removed		Disappeared		Total				
	Ylg	Ad	Total	Ylg	Ad	Ylg	Ad			Ylg	Ad	Total
Control												
1	1	3	4	0	0	0	0	0	0	0	4	4
4	1	2	3	0	0	0	0	0	0	0	3	3
9	2	1	3	0	0	1	0	1	0	0	2	2
Male and Female Removal												
2	1	4	5	0	2	0	0	2	2	2	3	5
3	2	3	5	1	2	1	0	4	1	1	1	2
Male Removal												
5	0	5	5	0	2	0	1	3	3'	2	3	5
8	1	8	9	0	3	0	1	4	4'	3	6	9
Female Removal												
6	2	3	5	0	0	1'	0	1	1	1	4	5
7	0	4	4	0	0	0	2	2	0	0	2	2
	10	33	43	1	9	3	4	17	11	9	28	37

' one adult moved to another section.
' one adult recruit.

Figure 7. Relationship between numbers of yearling male and female spruce grouse recruited on the core area at the onset of the breeding season, 1966 - 1981. Birds of unknown age were assumed to be yearlings.


NUMBER OF YEARLING MALES
NUMBER OF YEARLING FEMALES
0 1 2 3 4 5 6 7 8 9 10 11 12 13
67
71
72
78
74
66
70
68
79,80
73
61
r=0.758
P<0.0025

season.

Production

Production was examined by two methods. Chicks per female is a measure of reproductive success of females on the core area, and presumably the larger area from which juveniles immigrating onto the core area originate. Total number of juveniles on the core area is a measure of the availability of recruits. This last parameter is dependent upon reproductive success and number of resident females.

The relationship between mean number of chicks 4 weeks of age or older per resident female in a given year and number of yearling females recruited the next year was examined with a simple linear regression (Fig. 8). The slope, 6.33, was different from 0 (ANOVA, $F=8.980$, $P=0.024$). The relationship between number of juveniles on the core area in a given year and the number of yearling females recruited was also examined with a simple linear regression (Fig. 9). The slope, 0.19, was not different from 0 (ANOVA, $F=3.614$, $P=0.106$).

The relationship between mean number of chicks 4 weeks of age or older per resident female and number of yearling males recruited the next year was examined with a simple linear regression (Fig. 10). The slope, 4.65, was different from 0 (ANOVA, $F=7.700$, $P=0.032$). The relationship between number of juveniles on the core area and the number of yearling males recruited the following year was also examined with a simple linear regression (Fig. 11). The

Figure 8. Relationship between number of juvenile spruce grouse 4 weeks of age or older per resident female and number of yearling females on the core area the following year, 1966 - 1981. Only those years in which the number of juveniles 4 weeks of age or older per resident female was known were used. Two females of unknown age were assumed to be yearlings for 1967.

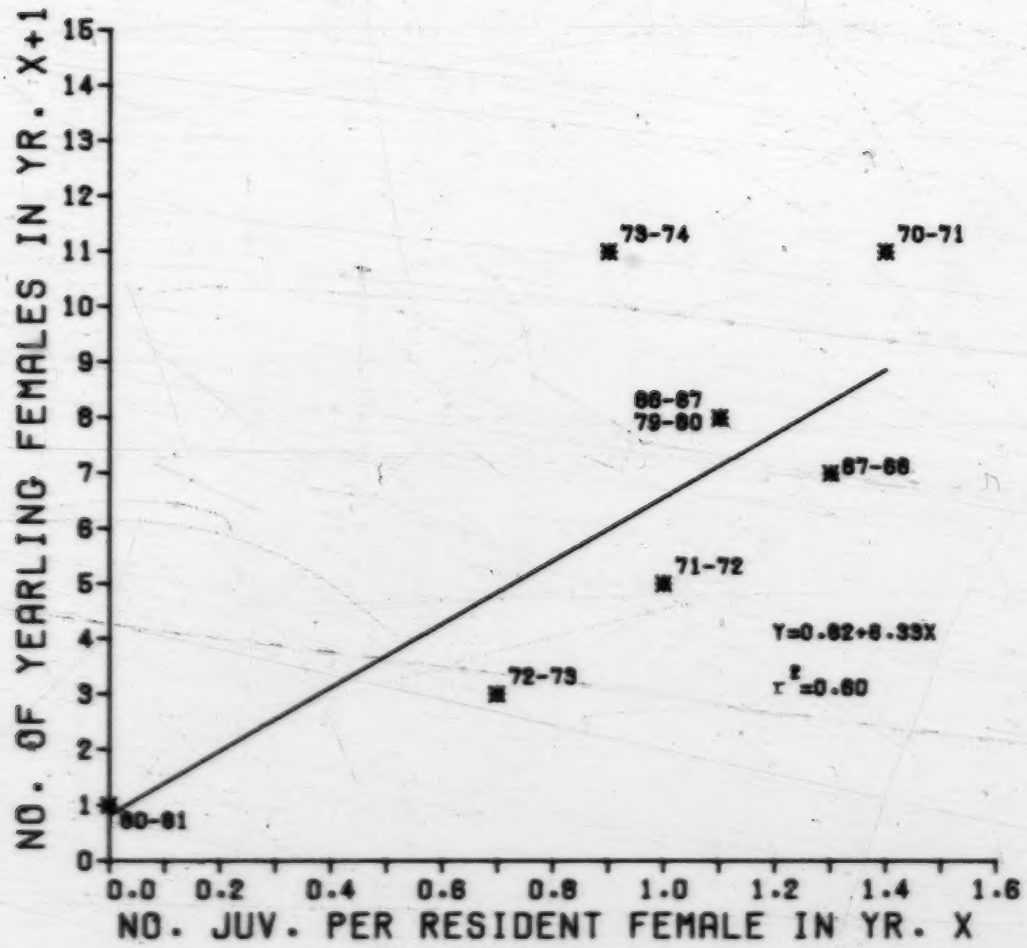

NO. OF YEARLING FEMALES IN YR. X+1
NO. JUV. PER RESIDENT FEMALE IN YR. X
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
73-74
70-71
66-67
79-80
67-68
71-72
72-73
80-81
Y=0.62+6.33X
r²=0.60

Figure 9. Relationship between number of juvenile spruce grouse 4 weeks of age or older on the core area and number of yearling females the following year, 1966 - 1981. Two females of unknown age were assumed to be yearlings in 1967.

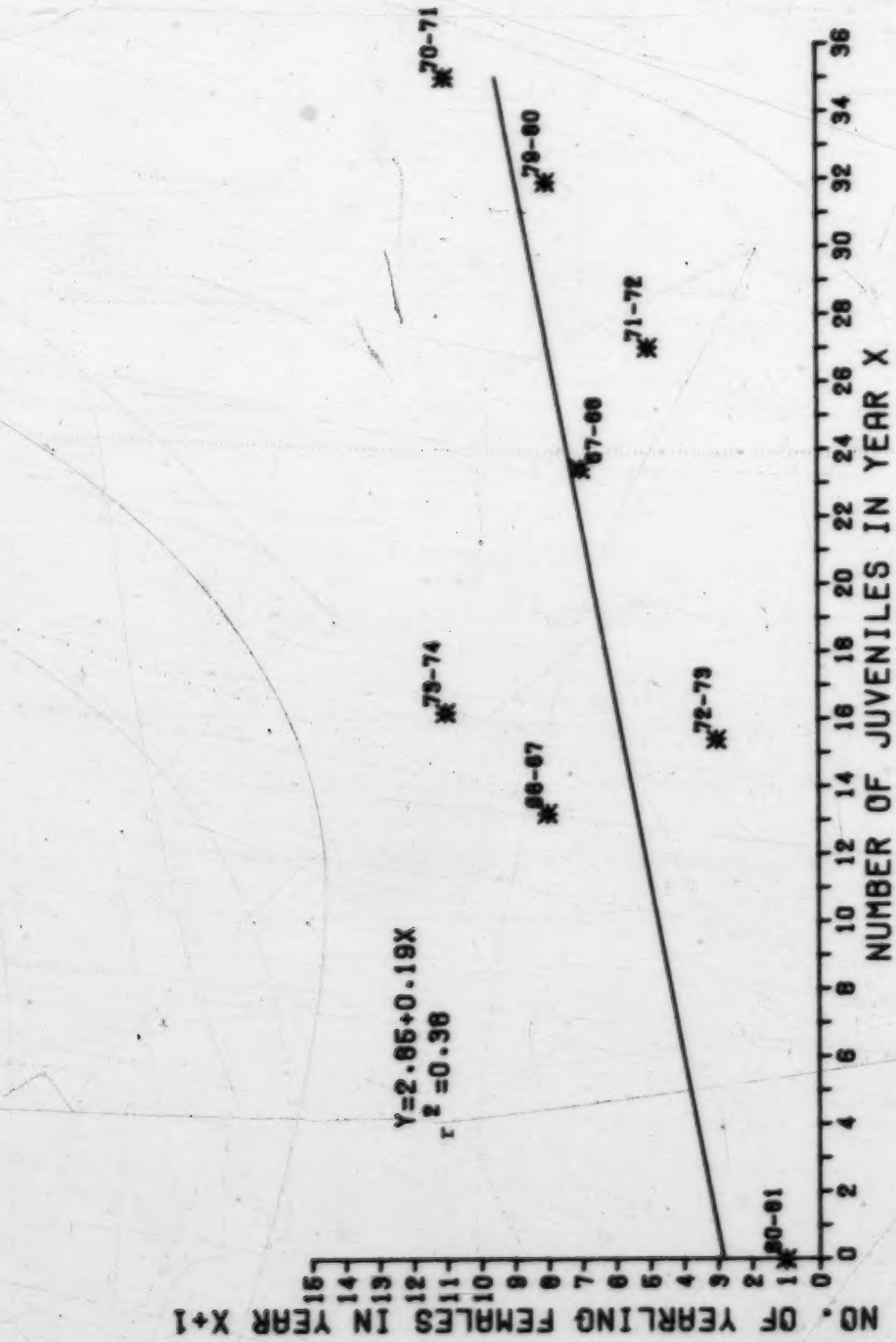

NO. OF YEARLING FEMALES IN YEAR X+1
NUMBER OF JUVENILES IN YEAR X
Y=2.85+0.19X
r² =0.38
80-81
88-67
73-74
72-73
67-68
71-72
79-80
70-71

Figure 10. Relationship between number of juvenile spruce grouse 4 weeks of age or older per resident female and number of yearling males on the core area the following year, 1966 - 1981. Only those years in which the number of juveniles 4 weeks of age or older per resident female was known were used. A male of unknown age was assumed to be a yearling in 1974.

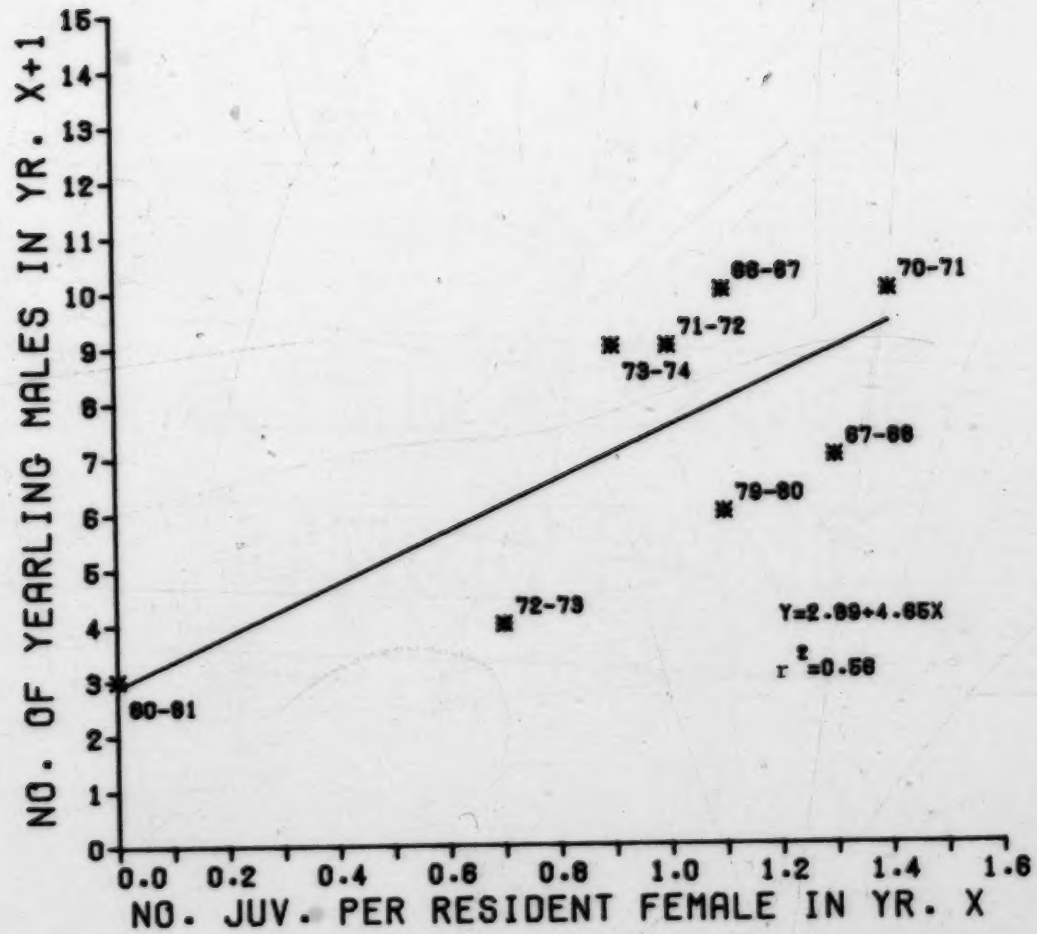
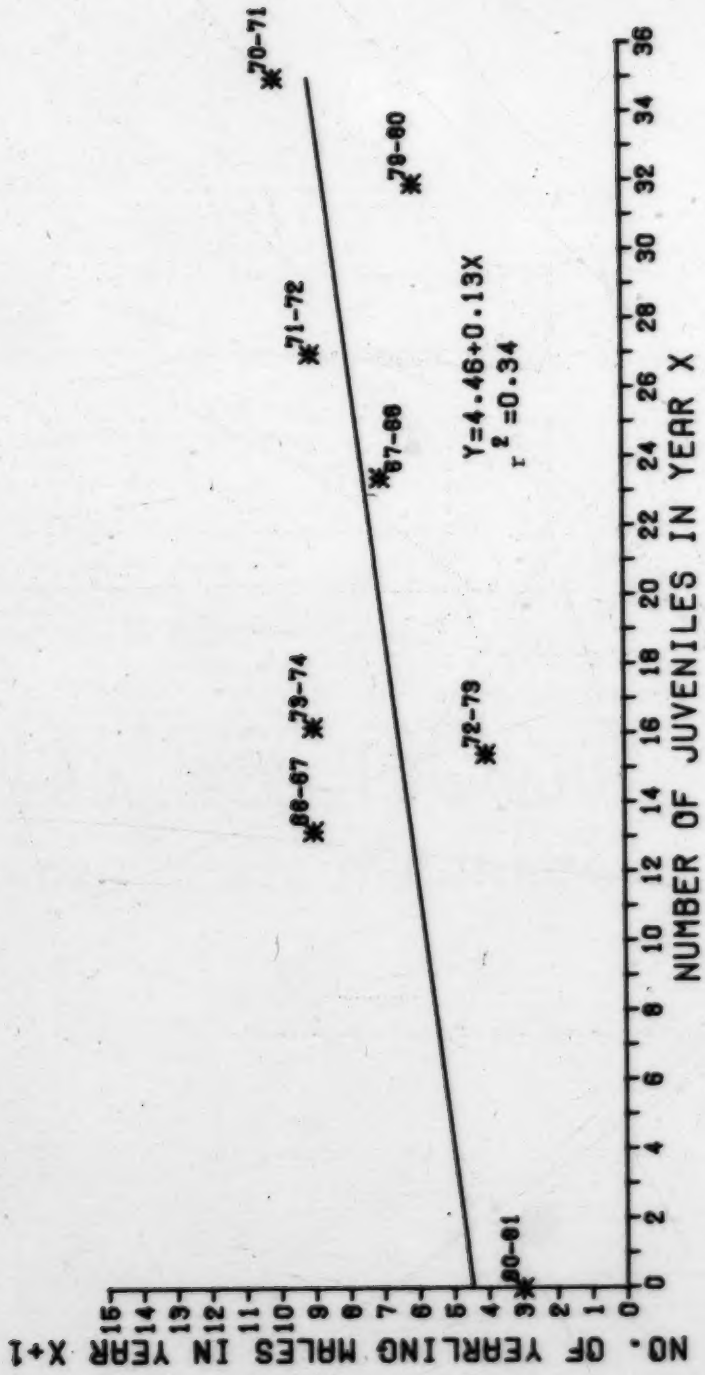

NO. OF YEARLING MALES IN YR. X+1
NO. JUV. PER RESIDENT FEMALE IN YR. X
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
66-67
70-71
71-72
73-74
67-68
79-80
72-73
60-61
Y=2.89+4.85X
r²=0.58

Figure 11. Relationship between number of juvenile spruce grouse 4 weeks of age or older on the core area and number of yearling males the following year, 1966 - 1981. A male of unknown age was assumed to be a yearling in 1974.


NO. OF YEARLING MALES IN YEAR X+1
NUMBER OF JUVENILES IN YEAR X
Y=4.46+0.13X
r² =0.34
66-67
73-74
72-73
71-72
67-68
70-71
78-80
80-81

slope, 0.13, was not different from 0 (ANOVA, F=3.022, P=0.133).

Territorial recruitment of male spruce grouse

The relationship between the number of territorial recruits (both yearling and adult) and established territorial males on the core area at the onset of the breeding season was examined with a simple linear regression (Fig. 12). The slope of -0.07 was not different from 0 (ANOVA, F=0.292; P=0.606). R^2, the proportion of variance in the number of territorial recruits explained by the number of established territorial males is 0.04. Based on this evidence, the number of territorial recruits (yearling and adult) at the onset of the breeding season appears to be independent of the number of territorial males.

The probability of recruitment into a subsection was the proportion of the total number of vacancies in that area. A computer simulation was conducted to determine if the observed distribution of recruits deviated significantly from the distribution expected from the spacing behaviour hypothesis. Probabilities of 0 (i.e. no vacancies) in any of the subsections result in an overall probability of 0 so it was necessary to eliminate data for 3 subsections (Table 3). The observed distribution that was used in the analysis was based on the remaining 7 territorial recruits in 6 subsections. Based on the probability of recruitment in each subsection, distributions of recruits were randomly

Figure 12. Relationship between numbers of newly recruited and established territorial male spruce grouse on the core area at the onset of the breeding season, 1967 - 1981.

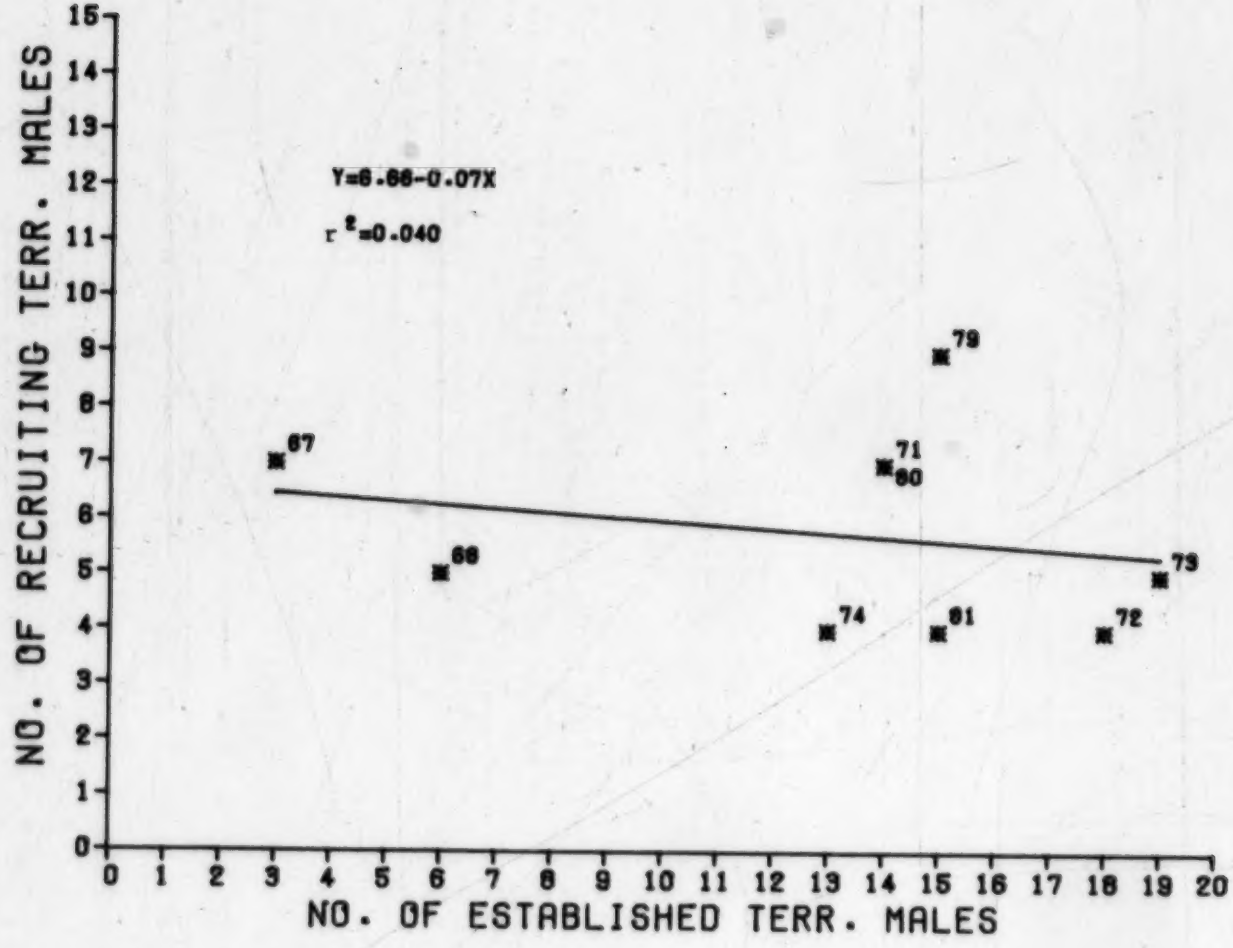

Y=6.66-0.07X
r²=0.040
NO. OF RECRUITING TERR. MALES
NO. OF ESTABLISHED TERR. MALES
67
68
71
80
79
74
81
72
73

Table 3. Number of territorial male spruce grouse removed and lost from and recruited onto various subsections of the study area, 1979 - 1980.

Subsection	Present in 1979	Lost			Recruited	Present in 1980
		Removed	Disappeared	Total		
Control						
1	4	0	0	0	0	4
4	2	0	0	0	1	3
9	2	0	1	1	1	2
Male and Female Removal						
2	4	2	0	2	2	4
3	4	2	1	3	0	1
Male Removal						
5	5	2	1	3	1	3
8	8	3	1	4	3	7
Female Removal						
6	3	0	0	0	1	4
7	4	0	2	2	0	2
	36	9	6	15	9	30

selected. 2,965 of the 10,000 simulated distributions had lower probabilities of occurrence than the observed distribution. This suggests that the observed distribution is not significantly different from the expected (P=0.2965). This result supports the spacing behaviour hypothesis.

The relationship between number of territorial recruits and number of nonterritorial resident males the previous year was examined with a simple linear regression (Fig. 13). The slope, 0.32, was not different from 0 (ANOVA, F=0.911, P=0.372). Based on this evidence number of territorial recruits at the onset of the breeding season does not appear to have been influenced by the number of nonterritorial resident males the previous year.

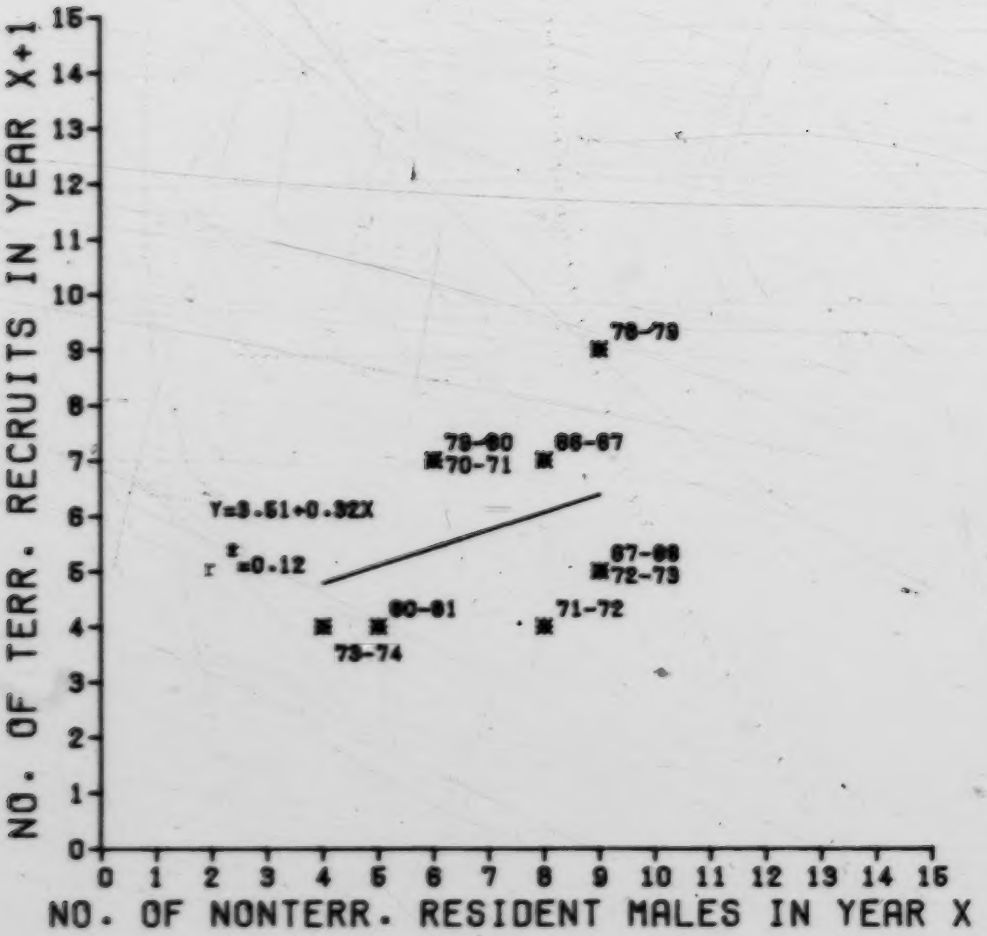
Discussion

Population dynamics

The number of spruce grouse in a population located in southwestern Alberta, has been monitored longer than any other population of spruce grouse. This population was in a period of growth between 1965 and 1971, followed by a relatively stable period between 1971 and 1981. The number of spruce grouse showed an approximate 2-fold change over the 17 year period (1965 - 1981).

Robinson (1980) reported that peaks of abundance occurred at 3-year intervals between 1965 and 1974 in a population of Canada spruce grouse (C. c. canace) in

Figure 13. Relationship between number of nonterritorial resident males and number of territorial recruits the following year.


NO. OF TERR. RECRUITS IN YEAR X+1
NO. OF NONTERR. RESIDENT MALES IN YEAR X
Y=3.51+0.32X
r²=0.12
78-79
79-80
70-71
66-67
67-68
72-73
80-81
71-72
73-74
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

Michigan. His evidence for the 1965 and 1968 peaks was based on census data, whereas evidence for the 1971 and 1974 peaks was based on incidental observations (Robinson 1980). Numbers of spruce grouse at the highest peak was 58 grouse and at the lowest trough 32 grouse, which is a 1.8-fold change in numbers. I suggest that Robinson (1980) does not have the critical data required to distinguish between cycles and random fluctuations about a mean.

Ellison (1974), who studied C. c. osgoodi in Alaska, recorded 14 (2.7/km²) to 19 (3.7/km²) male spruce grouse on a 2-square mile plot in May, 1965 - 1967. In 1969, 26 (5.0/km²) males were counted. Ellison (1974) considered the latter to be a minimum number because the census was conducted after males had stopped displaying and were more difficult to detect. This represents a 1.9-fold change in number of males. In the same study, the number of females on a 4-square mile plot was 39 (3.8/km²) from 1965 to 1967, and 65 (6.3/km²) in 1969, which is a 1.7-fold change. His data span too few years to allow one to interpret the significance of this increase.

All three populations of spruce grouse so far studied were relatively stable. However, the short-term nature of all these studies make this conclusion only tentative.

Population regulation

The relationship between the number of yearlings recruited as a percent of those available and the number of

adults on the study area was negative in both this study and that of Boag et. al (1979). My study is based on a much larger sample size (9 years vs. 3 years) and it considers males and females separately. This implies that a regulatory mechanism is operating in this population.

The closer the slope of the regression of numbers of yearlings and adults is to -1, the more stable the population. Stability can only be invoked as evidence of regulation if one can assume that the carrying capacity of the habitat has not changed during the course of this study. It is also necessary to assume that the effectiveness of spacing behaviour and territory size of the grouse has remained relatively stable among years. If these assumptions are valid the relationship between numbers of yearlings and adults can be used as a measure of the effectiveness of a regulatory mechanism. The lack of a significant inverse relationship between numbers of yearlings and adults of the same sex in this study implies that the regulatory mechanism does not maintain the population at a particular density but only moderates fluctuations.

Most adult male spruce grouse are territorial whereas most yearling males are nonterritorial (Herzog and Boag 1978). Brown (1969) argues that spacing behaviour of territory holders can not directly regulate the density of nonterritorial individuals. However, Zwickel (1980) provides experimental evidence that suggests the number of nonterritorial yearling blue grouse present on a block of

habitat may be regulated. Most yearling male blue grouse are nonterritorial, and the possibility that their numbers are regulated by territorial adults has not been ruled out (Zwickel 1980). Consequently, Brown's (1969) suggestion that it is not theoretically possible for nonterritorial individuals to be regulated by territory holders is questionable.

Removal study

Results of removal studies of blue grouse (Bendell et al. 1972, Zwickel 1972) suggest that density of adults can influence yearling recruitment. Similar trends were found in this study, but small sample sizes prevent me from making conclusive statements. However, I do consider the evidence supporting the spacing behaviour hypothesis to be fairly strong for males.

Because of the small number of birds within each subsection, I think the removal study should be repeated with the core area as the control and another area, approximately 200 - 250 ha, as the removal area. Most adults and yearlings (80 - 90%) should be removed in late summer from the experimental area, with recruitment of yearlings on the two areas compared the following year. Based on the results of this removal study, I predict that recruitment of yearlings will be greatest on the removal section.

Production

Boag et al. (1979) suggested that the number of juveniles surviving to September may influence the number of yearlings available as potential recruits the following year. Positive correlations between numbers of yearlings recruited and mean numbers of chicks per resident female the previous year, were statistically significant for both sexes. The correlations between chicks produced and resident yearlings the following year were also positive, though not significant.

Keppie (1979) reported that 56% of the yearling males and 93% of the yearling females that entered the population on the study area were raised elsewhere. Thus, the number of chicks raised in the general area, not just on the core area, determined the number of yearlings available for recruitment. Since Keppie's (1979) study area was 300 ha larger than the core area, these percentages are probably even higher for the core area. Changes in density of females on the core area are assumed to be representative of fluctuations in female density on the larger area from which recruits were drawn. This assumption may be invalid in some years. For example, in 1967 and 1974 more yearlings were recruited than were expected, based on the number of chicks the previous year and the trend set by the other 6 years. Perhaps the number of females on the core area, in 1966 and 1973 was an underestimate of female density on the general area. This dilemma remains unsolved. I suggest that

experimental manipulations of production are needed to help resolve this question.

Territorial recruitment of male spruce grouse

Two criteria must be satisfied to be able to claim that the territorial cohort is regulated by spacing behaviour (Klomp 1972): 1) some potential territorial recruits must be excluded by established territory holders. Keppie (1975) reported that yearling recruits on an adult removal area exhibited territorial behaviour. Similarly, in 1979, when there were five more adult territorial males than in 1981, fewer yearlings established territories (0 of 6) than in 1981 (1 of 3). This suggests that yearling males are potential territorial recruits that are excluded by resident territorial adult males); 2) exclusion must occur in a density-dependent manner for the density of territorial males to be regulated. The relationship between number of territorial recruits and established territorial males indicates that recruits are not excluded in a density-dependent manner. It is possible, however, that in some years sufficient yearlings were not present to fill the available vacancies. Territorial possession was based primarily on age, rather than on behaviour and some error in this method may have obscured a density-dependent relationship. Also it is possible that the assumption of a constant carrying capacity is invalid.

In summary, a positive correlation between the numbers of yearling females and males recruited suggests that both sexes are affected by the same factors or that these factors are correlated. The proportion of yearlings recruited of those available at the end of the winter appears to be regulated by density of adults of the same sex. This suggests that availability of recruits and number of adults of the same sex have influenced the number of yearlings recruited into the population. However, neither of these factors has an overriding affect since statistically significant results were not obtained when examined separately. Multiple regression analysis could not be performed because of small sample sizes. Such an analysis could be done in the future, after data are collected for additional years.

I was unable to show clear statistical relationships between number of territorial recruits and number of territorial males or number of nonterritorial residents the previous year. The distribution of territorial male recruits on the study area in 1980 was consistent with the spacing behaviour hypothesis.

CHAPTER 2. Dispersal histories, physical attributes, and age-specific survival rates of nonterritorial and territorial yearling male Franklin's spruce grouse

Introduction

Many studies of territoriality in tetraonids have been concerned with factors influencing rates of territorial recruitment (Watson and Jenkins 1968, Boag 1976, Lewis 1981). However, it is not known, apart from age, what determines the territorial status of a grouse. By comparing the characteristics of birds of the same age, yet different territorial status, one may discover why some individuals establish territories whereas others do not.

Among males of some tetraonids, successful territorial recruitment appears to be enhanced by large body size. Among sibling male red grouse (Lagopus l. scoticus), heavier birds are more successful in establishing territories than their lighter broodmates (Lance 1978). For ruffed grouse (Bonasa umbellus), Gullion (1981:376) reported that "if large enough, young males may even displace older established males".

Possession of a territory is probably a prerequisite for breeding in male grouse. If nonterritorial yearlings are reproductively immature, costs of territorial behaviour may outweigh the benefits. Active spermatogenesis does not appear to explain territoriality since it has been recorded in nonterritorial yearling male blue grouse (Dendragapus

obscurus) (Hannon et al. 1979) and sage grouse (Centrocercus urophasianus) (Eng 1963).

Androgen levels in the blood are related to aggressiveness in birds (Emlen and Lorenz 1942, Collias and Taber 1951, Selanger and Bermant 1967, Trobec and Oring 1972), which has been shown to influence the ability of individuals to establish territories at least in red grouse (Watson and Parr 1981). However, nonterritorial black grouse (Lyrurus tetrix) implanted with testosterone failed to establish territories (Johnstone 1969).

A higher mortality rate among territorial yearlings than among nonterritorial yearlings was proposed by Wiley (1974) as an explanation for postponed reproduction in male tetraonids. However, the mortality rates of nonterritorial adult male blue grouse are similar to those of territorial adult males (Lewis and Zwickel 1982).

The objective of my investigation was to examine some characteristics of yearling male Franklin's spruce grouse (Canachites canadensis franklinii) that might help to explain their territorial status. The following characteristics were considered: 1) dispersal distances, 2) body weights, 3) size and reproductive status of the testes, 4) amount of interstitial tissue in the testes, as a measure of androgen levels and 5)age-specific disappearance rates.

Methods

Data used in this study were collected from 1965 - 1981.

Classification of the territorial status of yearling males was based on size of area occupied (15 May - 15 August) and behaviour. In late spring (16 May - 9 June), territorial yearlings occupy areas similar in size to those of adults (mean=1.0 ha) but smaller than those of nonterritorial yearlings (mean=8.6 ha) (Herzog and Boag 1978). Size of areas occupied by territorial and nonterritorial yearlings in summer (11 June - 15 August) are unknown so the reliability of extending this criterion to 15 August is unclear. Wing claps and flutter flights are thought to function in advertising possession of a territory (Nugent 1979) and are only known to be performed by territorial birds (Herzog and Boag 1978). When data on both criteria were available, the greatest emphasis was placed on behaviour because it is considered to be a more reliable criterion.

Size of area occupied was based on an index, the standard diameter (sd), which was calculated as follows: $sd=(\Sigma d^2/n-1)^{\frac{1}{2}}$ (White 1964: 371). Diameter (d) is twice the distance between the location of a sighting and the mean location of all that male's sightings between 15 May and 15 August. In the formula, "n" represents the number of sightings. Since the denominator increases with the number of sightings there is no reason to believe that values of

this index are influenced by sample size other than being more reliable as "n" increases. A standard diameter (sd) was calculated for each yearling male sighted more than three times during the period (15 May - 15 August).

A simulation was conducted to test the reliability of the sd as a criterion for separating territorial and nonterritorial yearling males when only four sightings are available. Ten sets of four sightings were randomly selected from each yearling male that was located 15 times or more. A standard diameter was calculated for each set of four sightings and the territorial status of the bird was classified according to the value of the sd. The number of times that a bird's classification using four sightings was consistent with the classification based on all available sightings is a measure of the reliability of this criterion.

Males that were observed performing wing claps or flutter flights (MacDonald 1968) were considered territorial. Males that did not display in response to a playback of a female cantus (Nugent and Boag 1982) were considered nonterritorial.

A bird's dispersal distance was defined as the distance between the centre of a bird's brood range and the centre of the area it occupied as a yearling on its summer range (either as a territory or a home range). The centre of a home range or territory was estimated by a median location. This was the intersection of the median values of all the x and y coordinates of sightings for each individual. These

were plotted on a gridded aerial photograph of the study area. Only sightings recorded between 15 May and 15 August were used to avoid including locations of residents migrating to and from or on their wintering grounds. Brood sightings were those of the bird's brood hen from hatch date to 15 September or to the last sighting of that juvenile with its brood hen.

Body weight (±5 g) was measured with a 1500 g Pesola spring scale. Weights were compared only within certain time periods to reduce seasonal changes in weight as a factor (Pendergast and Boag 1973, Ellison and Weeden 1979). Late spring (16 May - 9 June) is the time when territorial yearling males can first be distinguished from nonterritorial yearling males (Herzog and Boag 1978). Winter-early spring weights were collected between 1 January and 15 May.

Three yearling males were equipped with solar-powered radio transmitters in 1981 (2 May, 18 May, and 28 May). Their locations were obtained every few days. On 6 and 7 June, these birds were located, captured and carried alive to the R. B. Miller Biological Station where they were killed with chloroform. Testes were removed and cleaned of extraneous tissue, and placed in 20 ml of Bouin's fluid. Two hours later two or three slices were cut in each testis to facilitate the penetration of the fixitive. Testis volumes were calculated by volumetric displacement to the nearest 0.01 cc. Total volume of testes was determined by summing

the volumes of the two testes for each bird. One testis from each bird was prepared for histological examination. Haematoxylin and eosin stains were used. These slides were then examined for the presence of spermatozoa and amount of interstitial tissue.

Amount of interstitial tissue in each testis was estimated. A camera lucida was used to superimpose a grid on a field under high power of a compound microscope. The proportion of each field underlain by interstitial tissue was determined by counting the number of squares that lay over this tissue and expressing this as a proportion of the total number of grid squares in the field. This procedure was repeated for 20 different fields, for each testis. The total amount of interstitial tissue was estimated by multiplying the proportion of interstititial tissue by the volume of a bird's testes.

Student's t-tests and Mann-Whitney U tests were used to compare dispersal distances, and physical attributes of territorial and nonterritorial yearling males. A Breslow test (Breslow 1970) was used to compare age-specific survival rates of males that took territories as yearlings and those that remained nonterritorial as yearlings. Differences were considered statistically significant if $P \leq 0.05$.

Results and Discussion

Territorial status

The frequency distribution of standard diameters of areas occupied by yearling males is shown in Figure 1. Males occupying space with standard diameters of more than 499 m were considered nonterritorial whereas those with standard diameters less than 376 m were considered territorial. Four of 46 yearlings (9%) occupied areas of intermediate size and were not classified as to territorial status nor used in further analyses.

The territorial status of a bird based on simulated sd's were sometimes inconsistent (5/42) with the results based on all available sightings (Table 1). These results suggest that using a standard diameter based on four sightings was a valid method for classifying the territorial status of a yearling male.

Classification based on size of area occupied was inconsistent with that based on behaviour in 6 of 17 cases for which behavioural data were available. Five males wing clapped and performed flutter flights but were nonlocalized according to the above criterion (sd's of 580 m, 605 m, 640 m, 825 m, 1205 m); these birds were considered territorial. One bird was relatively localized (sd of 320 m), but did not display in response to the female cantus and its home range overlapped the territory of an adult male; this male was considered nonterritorial. The territorial status of some yearling males may have been misclassified.

Figure 1. Frequency distribution of areas occupied by yearling male spruce grouse in southwestern Alberta (see text for description). Territorial males with standard diameters above 499 m or nonterritorial males with standard diameters less than 376 m were classified as such based on behaviour.

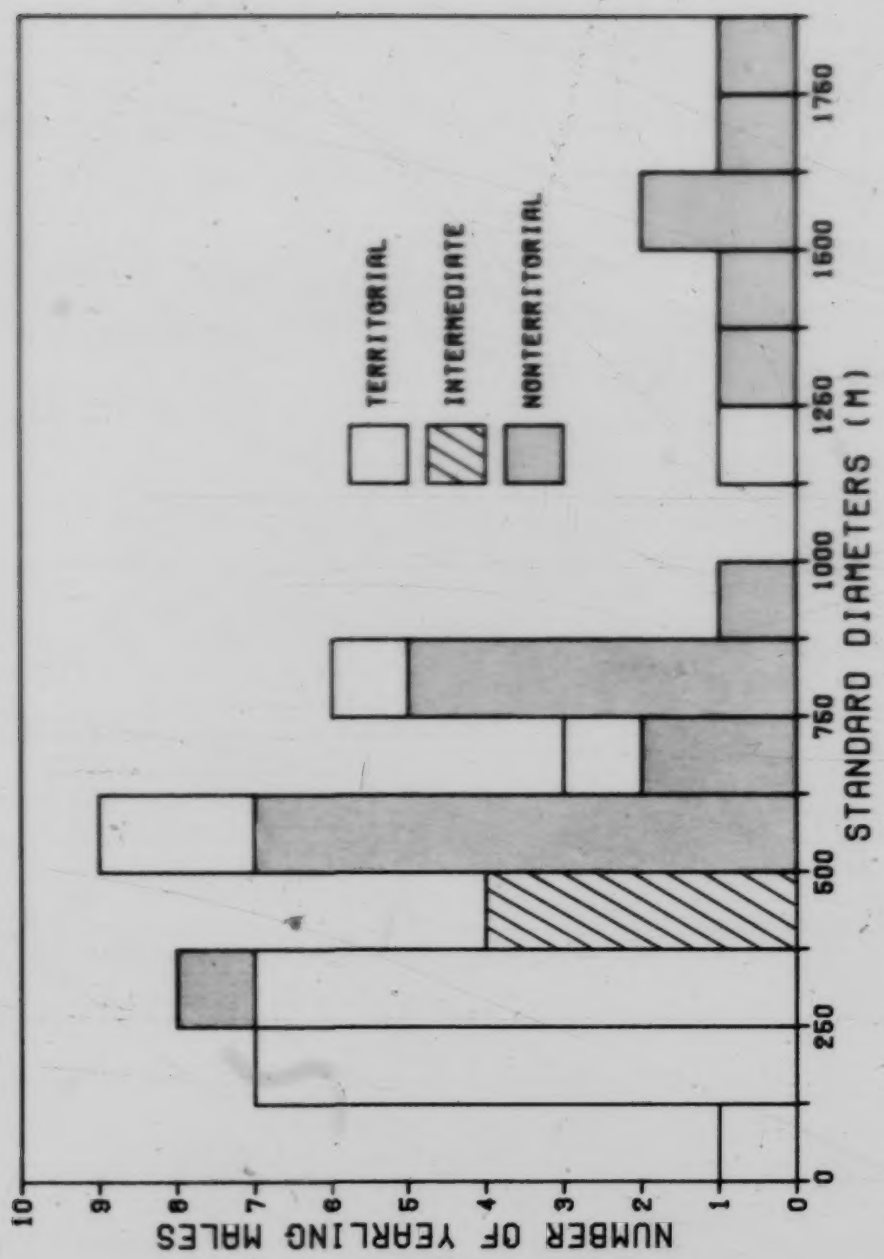

NUMBER OF YEARLING MALES
0
1
2
3
4
5
6
7
8
9
10
0
250
500
750
1000
1250
1600
1760
STANDARD DIAMETERS (M)
TERRITORIAL
INTERMEDIATE
NONTERRITORIAL

Table 1. Consistency of classification of territorial status of yearling male spruce grouse on sd's calculated from four randomly selected sightings and all (n) available sightings.

Yearling Male	Territorial Status	sd	n	Territorial status based on 4 randomly selected locations.		
				Terr.	Interm.	Nonterr.
1	Terr.	165	16	10	0	0
2	Nonterr.	585	33	2	2	6
3	Nonterr.	765	36	1	1	8
4	Nonterr.	580	37	1	4	5
5	Nonterr.	1205	38	1	1	8

Misclassification would reduce the likelihood of detecting differences between the groups of yearlings but increases confidence that differences, should they be found, were real.

Dispersal distance

The distance dispersed by territorial yearling male spruce grouse (mean=655 m) was significantly shorter than that moved by nonterritorial yearlings (mean=1161 m) (Table 2). These data may be biased because search efforts were concentrated on the study area and males that settled off this area were rarely located. The distance a bird had to disperse to leave the study area depended on the distance between its brood range and the boundary of the study area as well as the direction it dispersed. Thus, birds dispersing longer distances were more likely to settle off the study area and were probably under-represented. Distances moved during dispersal that are independent of the size of the study area are needed. Such data could be collected by radio tracking a sample of young birds.

Body weight

Variances of body weights of territorial and nonterritorial males were significantly different even after transformation (common log transformation, FMAX=25.67, df=8,4, $P<0.01$; square root transformation FMAX=27.32, df=8,4, $P<0.01$). A nonparametric test comparable to the 2-way ANOVA with replication is not available, so four

Table 2. Dispersal distances of territorial and nonterritorial yearling male spruce grouse.

Territorial Status	N	Dispersal Distances(m) Mean	SE	Difference'
Territorial	12	655	188	
				P=0.021
Nonterritorial	14	1161	129	

'Based on Student's t-test(2-tailed).

Mann-Whitney U-tests were conducted. The significance level for each Mann-Whitney U-test was reduced to 0.013 based on the Bonferonni equation (Kirk 1968). This was done to keep the overall significance level at 0.05.

In late spring (16 May - 9 June), when territorial and nonterritorial yearling males could first be distinguished, those with territory were significantly heavier (Table 3). However, there was no difference in the weights of these two groups during winter-early spring. The seasonal weight loss that occurred between winter-early spring and late spring was significant only among nonterritorial males. These results suggest that the subsequent weight difference is a consequence of territoriality rather than a reason for it.

Do the activities of territorial and nonterritorial yearling males differ in late spring? Territorial yearlings perform advertising and courtship displays and defend their territories against intruders. Ellison and Weeden (1979) suggested that these activities may be responsible for the weight loss recorded in male spruce grouse in Alaska during spring. Despite the fact that none of these presumably energetically-expensive behaviours is known to be exhibited by nonterritorial males, it is the nonterritorial group that showed the greater weight loss, in my study. Since such behaviour cannot be responsible for this greater weight loss, it may be related more to absolute distances moved per day. In late spring, nonterritorial yearlings are moving an average minimum distance of 334 m per day (Herzog and Boag

Table 3. Median body weights (gm) of territorial and nonterritorial yearling male spruce grouse. Similar superscripts indicate differences that are statistically significant.[1]

	Winter and Early Spring		Late Spring	
Territorial Status	N	Median	N	Median
Territorial	7	485	9	450[2]
Nonterritorial	9	465[3]	5	430[2,3]

[1]Differences tested using Mann-Whitney U-test(2-tailed).

[2]P=0.01

[3]P=0.005

1978), whereas adult territorial male spruce grouse are moving an average minimum distance of 70 m during the same period (Herzog and Boag 1978). Territorial yearlings were "behaving in all ways similarly to the adults" (Herzog and Boag 1978:857) by this time and so they probably move similar distances. Thus, greater distance moved by nonterritorial yearlings, possibly combined with more time spent alert and less time spent feeding than territorial yearlings, may be a greater energy drain that is manifested in greater weight loss.

Temporal variation in the seasonal weight reduction of nonterritorial and territorial yearling males is a possible explanation for the weight difference in late spring. Body weights of spruce grouse decrease between winter (December, January and February) and summer (June, July and August) (Pendergast and Boag 1973). The digestive tract, associated organs, and skeletal musculature are mainly responsible for the weight loss. A change in the mass of the digestive tract appears to be a consequence of a seasonal change in diet (lower rate of food processing associated with lower fiber content of ground vegetation-Fenna and Boag 1974). Ground vegetation is less fibrous than the winter diet of conifer needles (Pendergast and Boag 1971). Pendergast (1969) recorded cranberries (Vaccinium vitis-idaea) in the crops of spruce grouse as the snow melted. This suggests that spruce grouse feed on the ground vegetation as soon as snow-free areas appear in early spring. Snow accumulation and melt are

not uniform because of variation in the degree of openness and exposure, producing snow patches and snow-free areas during snow melt in early spring. If more snow cover occurs in areas occupied by yearlings which establish territories than in areas occupied by those which remain nonterritorial then a lower proportion of ground vegetation may be found in the diet of yearlings which establish territories. This would result in slower weight reduction of the digestive tract in territorial yearlings, so they would remain heavier than nonterritorial yearlings in late spring. However, the above must remain speculative until there is good evidence for it from the field.

Size and reproductive status of testes

Reproductive status does not appear to explain the occurrence of territorial and nonterritorial yearling male spruce grouse. Histological preparations of testes of yearling male spruce grouse showed that spermatozoa, the criterion used to identify a reproductively mature male, were present in both territorial (n=1) and nonterritorial (n=2) birds. However, presence of spermatozoa may not be an accurate measure of the fertility of a bird. Other factors such as production of low quantities or abnormal sperm may make a bird functionally infertile. Quality and quantity of spermatozoa produced could be determined by examining semen samples (Simard 1964).

Volume of testes of territorial and nonterritorial yearlings did not appear different. Testes of the one

territorial male were 0.20 cc in volume compared to 0.15 cc and 0.24 cc for the nonterritorial yearlings.

The amount of interstitial tissue in testes was used as an index of the amount of androgen produced (Pfeiffer and Kirschbaum 1943, Marshall 1949). The one territorial yearling had more interstitial tissue (0.005 cc) than either of the nonterritorial yearlings (0.001 cc and 0.002 cc). This suggests that territorial yearlings may be producing more androgen, and hence, be more aggressive. However, because the testes were examined after territorial recruitment the amount of interstitial tissue in the testes may have been the result of territory establishment, not the cause. Furthermore, with so few specimens these differences may only represent individual variation.

Age-specific disappearance rates

No statistically significant differences (Breslow statistic; P=0.64) were found in the age-specific disappearance rates of yearling males that took territories and those that were nonterritorial (Table 4). These results do not support Wiley's (1974) hypothesis which predicts higher mortality rates among territorial yearlings.

If disappearance rates are useful estimates of mortality rates for territorial and nonterritorial yearlings, the rate of movement off the study area must be similar in the two groups. The distances between areas occupied by individuals as yearlings and first year adults in the two groups were compared (Table 5). The shift in

Table 4. Age specific disappearance rates of male spruce grouse that established territories as yearlings and those that remained nonterritorial as yearlings.

	Age Class(years)									
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
Territorial										
Entered	30	17	11	6	5	4	2	1	1	1
Disappeared	12	3	4	1	0	1	0	0	0	1
Excluded[1]	1	3	1	0	1	1	1	0	0	0
Nonterritorial										
Entered	30	19	9	5	4	4	3	1	1	1
Disappeared	9	5	4	1	0	0	0	0	0	1
Excluded[1]	2	5	0	0	0	1	2	0	0	0

[1] Birds that were removed, killed accidentally or still alive in 1981, were excluded from calculations, in subsequent years.

Table 5. Displacement of central locations of areas occupied by spruce grouse as a yearling and as a first year adult.

Territorial status as a yearling	N	Displacement Distances(m) Mean	SE	Difference'
Territorial	10	131	29	
				P=0.0001
Nonterritorial	13	688	184	

'Based on Student's t-test(2-tailed).

location was significantly longer for nonterritorial (mean=688 m) than for territorial yearlings (mean=131 m). Thus, a greater proportion of nonterritorial than territorial males may have moved off the study area. The mortality rate of nonterritorial yearlings may be overestimated. Monitoring movements with radio telemetry would enable direct measures of mortality rates to be determined.

In summary, trends in the data suggest two hypotheses:

1) Yearlings that establish territories have higher blood androgen levels than nonterritorial yearlings. This hypothesis could be tested by collecting blood from yearlings before territorial establishment and comparing blood hormone levels of those that establish territories and those that remain nonterritorial. Testosterone proprionate and sham implants could be used to determine if there is a cause and effect relationship between androgen titers and territorial establishment. If yearlings that establish territories have higher blood androgen levels then research can be concentrated on why some birds have higher androgen titers than others.

2) Territorial yearlings disperse shorter distances than nonterritorial yearlings. This could be tested by radio-tracking dispersal movements of young male spruce grouse and determining their territorial status as yearlings.

More work needs to be directed towards comparing how social experience within the brood affects age of subsequent territorial establishment. Social rank in the brood, number of male siblings (Boag and Alway 1980) and heredity (Boag and Alway 1981) are areas that appear to warrant particular attention.

CONCLUDING DISCUSSION

Boag et al. (1979) presented a working hypothesis, postulating how regulation of numbers could be achieved in spruce grouse populations. They suggested that as density of resident grouse increased production decreased, which was a "coarse tuning" mechanism and spacing behaviour in the spring acted as the "fine tuning" mechanism that held density near the carrying capacity of the habitat.

Smyth (1983) reexamined the relationship between production and density of females during the breeding season with additional years data. Her data did not support the negative relationship as postulated by Boag et al. (1979). Thus female density does not appear important in regulating production in this population.

I reexamined the relationship between the number of adults and number of yearlings of the same sex recruited into the local population. Data from this study suggest that as the number of adults increased the percentage of yearlings recruited of those available decreased. However, the relationship between numbers of yearlings and adults was not statistically significant for either sex. Thus this regulatory process appears to modify fluctuations rather than maintain the population at a specific number.

Proportion of available recruits and not actual numbers of yearlings was regulated. Thus factors influencing the availability of potential recruits prior to spring dispersal can affect the number of yearlings actually recruited.

Keppie (1979) provides evidence that number of yearlings prior to spring dispersal is a function of production the previous year. Variation in overwinter survival could also influence number of yearlings present at this time. However, survival appeared to be relatively stable in the three winters monitored by Keppie (1979).

One aspect of recruitment that Boag et al (1979) did not incorporate in their working hypothesis was territorial recruitment of males. In order for spacing behaviour of territorial males to operate as a regulatory mechanism some potential recruits must respond by remaining nonterritorial or establishing a territory elsewhere when a surplus of potential recruits exists. Only yearlings are known to be nonterritorial. Is this a response to spacing behaviour? Yearlings on an adult removal area exhibited territorial behaviour (Keppie 1975). This suggests that the nonterritoriality of at least some yearlings is a response to the spacing behaviour of adults.

Why most adult males territorial whereas some yearling males remain nonterritorial? that there is a shortage of suitable territorial space, one explanation is that adults are dominant over yearlings. An alternative explanation is that adults take territories earlier than yearlings and once they have established a territory can successfully defend it against intruders. Some adults established their territories the previous fall (unpublish. data, Robinson 1980) as yearlings and thus settled in vacancies before the younger

birds could. Similarly, if recrudescence of testes in adults were earlier than for yearlings this would facilitate the establishment of territories by adults sooner in the spring. This hypothesis could be tested by monitoring the movements of young birds and determining when territories are established.

Why do some yearling males establish territories whereas others do not? Yearlings might only establish a territory if a high quality site is available. A bird might be better able to assess the quality of a site by observing the intensity of displays or some other characteristics of previous occupants of a site in the fall as a juvenile or in the early spring as a yearling. This might explain why nonterritorial birds are attracted to displaying males (Nugent 1979). If a vacancy is available in an area familiar to the yearling and this site is of suitable quality it might attempt to establish a territory there. However, if no vacancies or only sites of poor quality are available in their "area of familiarity" they may move to an unfamiliar area. If a space is available in an unfamiliar area a bird may not be able to adequately judge the quality of a vacant space in time to breed that year and thus foregoes territoriality until this can be done.

This hypothesis could be tested in several ways. The "area of familiarity" of young birds could be determined by monitoring their movements. Yearlings should establish territories in these "areas of familiarity" more frequently

than in other areas. Another approach would be to remove territorial males on some sites but not others. This would be continued until none of the nonterritorial birds were likely to have had contact with previous occupants of the removal sites. A complete removal could then be done and recruitment compared on the recently occupied and vacant sites. This hypothesis predicts that recruitment of yearlings would be earliest and greatest on the control or recently occupied sites. A similar scenario is possible without potential territorial recruits using previous occupants to assess the quality of territorial space.

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